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**ROOT HERBIVORY IN GRASSLANDS AND SAVANNAS: THE POTENTIAL ROLE OF JUNE BEETLE (*PHYLLOPHAGA SPP.*; SCARABAEIDAE) LARVAE IN CENTRAL TEXAS PLANT COMMUNITY STRUCTURE**

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by

**Michael Shawn Brumbaugh, B.S.**

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For Jennifer, Zoe, and ‘the kid’.

You are the Joy in my life and just the thought of you makes me smile.

Also for my parents

who showed me the world and taught me to love wild places.

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**ROOT HERBIVORY IN GRASSLANDS AND SAVANNAS: THE POTENTIAL ROLE OF JUNE BEETLE (*PHYLLOPHAGA SPP.*; SCARABAEIDAE) LARVAE IN CENTRAL TEXAS PLANT COMMUNITY STRUCTURE**

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Aboveground herbivores play an important role in plant community processes; however the role of belowground herbivory has received little attention. This is a study on root herbivory by June beetle (*Phyllophaga spp.*; Scarabaeidae) larvae in grasslands and savannas in central Texas. I begin by presenting a descriptive survey of *Phyllophaga spp.* larvae in central Texas grassland and savanna sites (Chapter 1). Larval density was generally low and patchy within and among sites. Furthermore, I found that larval abundance was positively associated with forb vegetation and negatively associated with grasses. Stable carbon isotope analysis revealed that larvae selectively fed on forbs over

grasses at one site, but larvae exhibited no preferential feeding at the other sites. I then describe a greenhouse study that investigated the feeding preference of *Phyllophaga crinita*, the most common *Phyllophaga* species in Texas, for co-occurring plant species (Chapter 2). Specifically, I observed larval feeding in a two-choice feeding environment that neighbored individuals of the native bunchgrass, *Schizachyrium scoparium* (little bluestem grass) with individuals of the exotic grass, *Bothriochloa ischaemum* (King Ranch bluestem), and with individual seedlings of the native woody species, *Prosopis glandulosa* (honey mesquite), and *Juniperus ashei* (Ashe juniper). *Phyllophaga* larvae preferred *Schizachyrium* over both woody species, but larvae showed no distinction between the two grass species. *Schizachyrium* size was also negatively related to the extent that it was preferred over its neighbor. Lastly, I present the findings of a garden study that examined the effect of root herbivory by *Phyllophaga* larvae on the competitive interaction between *Schizachyrium* and *Prosopis* seedlings (Chapter 3). In doing so, I conducted separate experiments in successive years that varied the density of larvae and *Schizachyrium* competitors in pots. There was no evidence that root herbivory altered the ability of *Schizachyrium* to competitively suppress *Prosopis* growth. Instead, at high density *Phyllophaga* larvae had a strong direct negative effect on both *Prosopis* and *Schizachyrium* performance. At lower densities, however, these herbivores caused similar moderate reductions in both plant species, and as a result *Prosopis* performance was primarily impacted by the strong competitive effect of *Schizachyrium*.

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## Overview

Even though aboveground herbivores are known to play an important role in the composition and structure of grasslands and savannas, the role of belowground herbivores has received little attention and is poorly understood. The goal of this study was to determine the potential effects of *Phyllophaga spp.* (June beetles) larvae, which are root-feeding insects, commonly called white grubs, on the species composition and structure of grasslands and savannas in central Texas.

In Chapter 1, I present a descriptive survey of white grub abundance and the vegetation composition in grassland and savanna sites in central Texas. In this chapter, I also used stable carbon isotope analysis to examine the relative contribution of grass ($C_4$) and non-grass ($C_3$) species to grub diet. In Chapter 2, I conducted a greenhouse experiment to examine the feeding preference of *Phyllophaga crinita*, the most common species of white grub in Texas, for common co-occuring plants, and whether its feeding behavior affected the performance of *Schizachyrium scoparium* (little bluestem), a native dominant grass. Lastly, Chapter 3 examines the effect of *Phyllophaga spp.* larvae on the competitive interaction between *S. scoparium* and seedlings of *Prosopis glandulosa*, an invasive native woody plant.

I surveyed the vegetation and white grub abundance at 12 sites on the eastern Edwards Plateau in central Texas (Chapter 1). White grub density was generally low (compared to outbreak densities) and patchy both within and among sites. White grub abundance was also positively associated with forb vegetation and negatively associated with grasses. Stable carbon isotope analysis of larvae indicated that the dietary contribution of grasses ($C_4$) and forbs ($C_3$) differed among sites independent of vegetation composition. In particular, there was evidence that larvae at one location selectively foraged on forbs over grasses, although at other grassland and savanna locations there was no indication of preferential feeding.

In Chapter 2, I describe a greenhouse experiment that investigated the feeding behavior of *Phyllophaga crinita*, the most common white grub species in Texas, in a two-choice feeding environment that paired individuals of *Schizachyrium scoparium* (little bluestem), a native dominant bunchgrass, with individuals of three invasive species in central Texas: *Bothriochloa ischaemum* (King Ranch bluestem grass), *Prosopis glandulosa* (honey mesquite), and *Juniperus ashei* (Ashe juniper). *P. crinita* larvae showed a strong and moderate preference for *S. scoparium* over the two woody species, *J. ashei* and *P. glandulosa*, respectively. In contrast, there was no indication of selective foraging by *P. crinita* between *S. scoparium* and the other grass species, *B. ischaemum*. In accordance with *P. crinita* feeding preference, *S. scoparium* plants were smallest when neighbored with *J. ashei*, largest when neighbored with *B. ischaemum*, and were intermediate in size when neighbored with *P. glandulosa*. There was no discernable difference in the size of *S. scoparium* plants grown with *B. ischaemum* and those in 'control' pots without either neighbors or *P. crinita* larvae, indicating that *S. scoparium* was able to compensate for low levels of root herbivory.

Lastly, I investigated the separate and joint effects of competition and root herbivory by *Phyllophaga spp.* larvae on *S. scoparium* and *P. glandulosa* seedling performance in two separate experiments conducted over successive years (Chapter 3). I chose these plant species because of the potential implication for *P. glandulosa* encroachment into grasslands and savannas. In the first experiment, I studied the effects of high intensity root herbivory (four larvae per pot) on *P. glandulosa* seedlings grown in an additive competition experiment with *S. scoparium* (0, 1, and 3 neighboring grass plants per pot). In the second experiment, I examined the effects of low to moderate herbivory intensity (0, 1, and 2 larvae per pot) on both *P. glandulosa* seedlings and *S. scoparium* individuals grown alone and together. There was no evidence that root herbivory modified the ability of *S. scoparium* to competitively suppress *P. glandulosa* growth in either experiment. At high density *Phyllophaga* larvae had a strong direct negative effect on both *P. glandulosa* and *S. scoparium* performance. In contrast, at lower densities, these herbivores caused similar moderate reductions in both *P.*

*glandulosa* and *S. scoparium* size, and as a result *P. glandulosa* performance was primarily impacted by the strong competitive effect of *S. scoparium*.

In conclusion, this study is one of only a few that examine the role of insect root herbivory in natural grassland and savanna systems, and to my knowledge, it is the only study that explicitly investigates the effect of root herbivory on grass-woody seedling competition in the context of woody plant encroachment. The findings reported in this dissertation suggest that during outbreak years white grubs can be a significant form of belowground disturbance, yet in non-outbreak years the effect of these insects may be subtle and subordinate to the effects of plant competition (Chapter 3). However, the results in Chapters 2 and 3 suggest that the effects of white grubs on community composition of grasses and forbs, and on the possible encroachment by other woody species (e.g. *J. ashei*), are likely to be complex and dependent on several factors. Specifically, species of white grubs may differ in female oviposition preference and larval feeding habits which will affect their abundance and impact on plant species composition in grassland and savanna patches. In addition, the effect of white grubs on plant interactions may depend on the attributes of neighboring plants such as palatability, compensatory growth ability, and competitive status. Further study of these factors is needed to better understand the role of white grubs (*Phyllophaga spp.*), and other belowground herbivores, in grassland and savanna community dynamics.

# Chapter 1: A descriptive survey of white grubs (Coleoptera: Scarabaeidae) in central Texas grasslands and savannas and an analysis of diet using stable carbon isotope signatures.

## Introduction

Herbivores are thought to play an important role in community and ecosystem processes in many grasslands and savannas (Dyer et al. 1982, Crawley 1983, McNaughton 1983, Detling 1988, Archer 1994, Van Auken 2000). Most studies have focused on the effects of vertebrate grazing, and belowground herbivory has received relatively little attention (Crawley 1983, Andersen 1987, Brown and Gange 1990, Hunter 2001). However, most of the net primary production and plant biomass is underground in many grasslands and savannas (Coleman 1976, Sims and Singh 1978, Jackson et al. 1996), soil resources are often limiting in these systems (Fowler 1986), and the consumption of plants by subterranean invertebrates can be greater than that of aboveground mammals (Smolik et al. 1976, Scott et al. 1979, Stanton et al. 1981, Ingham and Detling 1984). Furthermore, the effects of belowground herbivory on plant communities can be quite different from those of aboveground herbivores (Brown and Gange 1989a).

Many species of Scarabaeidae (Coleoptera), most notably *Phyllophaga spp*. (June beetles), have root-feeding larvae, commonly called white grubs, that cause significant damage to rangelands, grass crops, and turfgrasses (Graber et al. 1931, Schumacher 1959, Teetes 1973, Ueckert 1979, Merchant and Crocker 1995, Rodriguez del Bosque et al. 1995, Potter 1998). Hewitt et al. (1974) noted that *Phyllophaga spp*. (June beetles) are among the most destructive soil insects in rangelands and even their infrequent outbreaks can have long-term consequences for plant community structure (Coffin et al. 1998). However, we know little about the abundance and feeding activities of these potentially important herbivores in grasslands and savannas, especially during non-outbreak

conditions (Brown and Gange 1990). Because of the difficulties in observing the feeding activities of herbivores underground, the belowground activities of herbivores are often merely inferred from aboveground responses. The effect of low or moderate intensity herbivory underground may often go unnoticed or may be attributed to other biotic factors (e.g. competition) or abiotic stress (e.g., drought) (Hewitt et al. 1974, Davidson 1979).

This study presents a descriptive survey of root-feeding scarabaeid larvae (hereafter also referred to as white grubs) in 12 grassland and savanna sites located in central Texas. Specifically, I investigated (1) the range of larval densities among sites and (2) whether larvae were associated with grass and forb cover. I also used stable carbon isotope analyses to determine (3) whether larvae fed preferentially on grass or non-grass species (i.e., forbs and woody plants). White grubs are known to affect primarily grass species (Andersen 1987, Hewitt et al. 1974, Clements 1984). For example, reports of white grubs (*Phyllophaga spp.*) as agricultural pests pertain to grass crops (e.g. wheat, sorghum, sugarcane) and turfgrasses (Teetes 1973, Merchant and Crocker 1995, Potter 1998) and white grub outbreaks in rangelands have been reported to cause a decrease in grass cover (Schumacher 1959, Anonymous 1969, 1971b) and an increase in forb cover following disturbance (Ueckert 1979, Coffin et al. 1998). Therefore, I hypothesized that white grubs are more abundant in locations with greater grass dominance, and that they feed selectively on grasses over forbs.

Stable carbon isotope analysis provides a powerful tool for tracing energy flow in food webs and determining the diets of animals (Petelle et al. 1979, Tieszen and Boutton 1989). Its use can be particularly helpful in belowground studies (Boutton et al. 1983) where the direct observation of organisms is difficult. Because the ratio of stable carbon isotopes (i.e. $^{13}C$ / $^{12}C$) of animals reflects closely that of their diet (DeNiro and Epstein 1978, Peterson and Fry 1987) it can be used determine the relative consumption of plant species or plant functional types that differ in their isotopic compositions. In particular, $C_3$ plants are more depleted in $^{13}C$ ($\delta^{13}C$ mean ca. –27‰) than $C_4$ plants ($\delta^{13}C$ mean ca.

–13‰) (Farquhar et al. 1989a, Tieszen and Boutton 1989) due to different discrimination against the heavier $^{13}CO_2$ molecule by the carbon fixing enzymes involved in the different photosynthetic pathways. Grasslands and savannas of the eastern Edwards Plateau of central Texas are comprised primarily of $C_4$ grasses and $C_3$ forbs and woody species (Fowler and Dunlap 1986). As a result, the stable carbon isotopic signature of white grubs will reflect the dietary contribution of these two plant functional types. Using a two-part mixing model (Fry et al. 1978, Tieszen and Boutton 1989, Boutton et al. 1998), I calculated the expected isotopic signature of larvae under the null hypothesis that they fed on $C_4$ grasses and $C_3$ forbs in proportion to their abundance in the foraging environment estimated from aboveground cover. Significant deviations in observed $^{13}C/^{12}C$ values from these expected values would indicate that the larvae were selectively feeding on the $C_4$ grasses or the $C_3$ forbs and woody species.

## Methods

### *White grub survey*

I sampled white grubs (scarabaeid larvae) at 12 sites located in Travis and Burnet Counties in central Texas between February and April in 2001. All of the sites were on the eastern Edwards Plateau. The vegetation in this region is a mosaic of grasslands, savannas and oak-juniper woodlands (Fowler and Dunlap 1986, Amos and Gehlbach 1988). The climate of this region is subhumid and the area receives approximately 83 cm annual rainfall. The wettest periods are usually May and September, but rainfall is highly variable (National Weather Service, recorded at Camp Mabry, Austin, TX).

To determine the relative contribution of grass and non-grass plants to larval diet using stable carbon isotope analysis (described below), I surveyed areas where grasses were almost exclusively $C_4$ species; all non-grass plants were $C_3$ species. Specifically, site selection criteria were (1) grassland or savanna vegetation dominated by

*Schizachyrium scoparium* (little bluestem grass), a native $C_4$ perennial grass, (2) $C_3$ grasses (in particular, *Nassella leucotricha*, Texas wintergrass) absent or infrequent and (3) soils >20 cm in depth. I selected sites that were at least several miles distant from every other site, except for the two Slaughter sites (Tract and Cemetery) which were about 0.25 miles from each other, and the two sites at Shield Ranch (Chalk Hill and Ungrazed) which were about 1 mile from each other. Even though these sites were relatively close to each other, they did differ in soil type (see Fig. 1.1 for site locations and Appendix A for site descriptions). At each site, I randomly located five 10 m x 10 m plots. All plots were in open grass-dominated areas. Within each plot, I randomly sampled 10 1m x 1m subplots, giving a total of 50 sampling locations per site (5 plots x 10 subplots/plot per site). In each subplot I visually estimated the absolute percent cover of all standing plant tissue (dead and alive), the absolute percent cover of grasses, and the absolute percent cover of non-grass plants. Non-grass plants consisted mainly of forbs and hereafter are referred to as such, although woody seedlings and small shrubs were occasionally found in or near subplots. Cover was scored using the following cover classes: 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, 4 = 75-100%. I sampled larvae by excavating a core of soil (15 cm diam. x 20 cm deep) from the center of each subplot and carefully sorting through the excavated soil. Larvae were collected, frozen, and weighed. I assigned each larva to a size class: small (<0.15 g), medium (0.15-0.50 g) and large (>0.50 g). During soil excavation, many larvae (~ 40%), especially the smallest ones, were damaged and could not be weighed. For each of these larvae, I visually estimated size class.

***Stable carbon isotope analysis***

I selected 5-9 larvae from each of five sites for stable carbon isotope analysis. All larvae were either medium or large in size, and were dried and ground. $^{13}C/^{12}C$ ratios of larvae and plant tissues were analyzed at Duke University's Environmental Stable

Isotope Laboratory with a Finnigan MAT Delta Plus XL mass spectrometer (Thermo Finnigan, San Jose, CA). All values are relative to the international V-PDB (Peedee Belemite) standard by calibration through NBS-22 (Craig 1957, Qi et al. 2003). Stable carbon isotope ratios are expressed as $\delta^{13}C$ where:

$$\delta^{13}C = \left[ \frac{^{13}C/^{12}C \text{ sample} - {}^{13}C/^{12}C \text{ Standard}}{^{13}C/^{12}C \text{ Standard}} \right] \text{ X } 1000 \quad \text{[Equation 1].}$$

Because plant tissues have relatively less $^{13}C$ than the standard, $\delta^{13}C$ values for isotope ratios are negative.

I compared the $\delta^{13}C$ of larvae with $\delta^{13}C$ values calculated using a two-part mixing model under the null hypothesis of no selectivity in diet. In this null model I assumed that larvae consumed the $C_4$ grasses and the $C_3$ plants in proportion to their availability to larvae (i.e. that there was no preferential feeding). Relative proportional cover was used as a surrogate for root availability. I assumed that all plants within the 1 $m^2$ subplot were equally available. I calculated the predicted $\delta^{13}C$ of larvae by the mass balance equation:

$$\delta^{13}C = (\delta^{13}C_{C4})(x) + (\delta^{13}C_{C3})(1\text{-}x) \qquad \text{[Equation 2],}$$

where $\delta^{13}C_{C4}$ is the average $\delta^{13}C$ value of $C_4$ species' roots, $x$ is the relative proportion of $C_4$ (grass) cover, $\delta^{13}C_{C3}$ is the average $\delta^{13}C$ value of $C_3$ species' roots, and $1\text{-}x$ is the relative proportion of $C_3$ (forb) cover. I used average $\delta^{13}C$ values of –14.0‰ for $C_4$ grasses and –29.4‰ for $C_3$ plants as reported by Boutton et al. (1998) for grasses and forbs, respectively, in a south Texas savanna. The fractionation of $^{13}C$ in the assimilation of carbon by these larvae is not known, but the fractionation by animals is generally low (< 1‰) (Peterson and Fry 1987).

To calculate the relative proportion of $C_4$ grasses ($x$) and $C_3$ forbs ($1\text{-}x$) available to each larva, I used the mid-values of the absolute percent cover range associated with the grass and forb cover classes of the subplot where the larva was collected. For

example, with a grass cover class of 4 (75-100% absolute cover) and a forb cover class of 2 (25-50% absolute cover), the relative proportion of grass cover ($x$) would be [87.5 / (87.5+ 37.5)] = 0.70, and the relative proportion of forb cover (1-$x$) would equal 0.30. Using these estimates in Equation 2, the $\delta^{13}C$ value expected under the null hypothesis would be –18.6‰.

To establish reference values of $\delta^{13}C$ for larvae with diets exclusively of $C_4$ or $C_3$ plants, I collected first instar *Phyllophaga spp*. in an area dominated by *Cynodon dactylon* (a $C_4$ grass) within the experimental garden at Brackenridge Field Laboratory (BFL), Austin, Texas. Twenty larvae assigned a $C_4$ diet were placed in pots (two larvae per pot) with *Schizachyrium scoparium* (a $C_4$ grass) that I grew in a greenhouse. Twenty larvae assigned a $C_3$ diet were kept in containers filled with moist sand and fed sweet potato (*Ipomoea batatas*). Roots from *S. scoparium* grown in an outdoor garden experiment at BFL were analyzed for $\delta^{13}C$. The $\delta^{13}C$ value of sweet potato (–29.8‰) is reported by Kelm et al. (2000). After five months, I randomly selected three third instars of similar size from each diet treatment for isotope analysis. These third instar larvae were approximately 5-7 times larger than when collected as first instars.

***Statistical Analyses***

I used SAS v8.0 (SAS Institute 1999) for all statistical analyses.

*White grub density*

For each site separately, I first summed the number of larvae in all 10 subplots in each plot, and then averaged these sums to obtain the average density of larvae per plot in that site.

*Vegetation cover*

I first calculated, for each subplot, the difference between its grass cover score and its forb cover score, to obtain the new variable 'cover difference'. Each subplot thus had four cover variables: total cover, grass cover, forb cover, and cover difference. Next, for each of these four variables separately, I averaged the values of the 10 subplots in each plot, yielding a data set with 60 observations (N=60 plots) and four variables per observation. Finally I averaged the values of the 5 plots in each site, yielding a data set with 12 observations (N = 12 sites) and four variables per observation. Because this final data set has only one observation (of four variables) per site and the larval density data set also has only one observation per site, pseudo-replication is avoided.

*The relationship between white grub density and vegetation*

I used Spearman's rank correlation coefficient to test the relationship between the mean larval abundance in a site and each of the cover variables (plant, grass cover, forb cover, and cover difference [= grass cover – forb cover]) in that site.

*Effects of vegetation on isotope ratio ($\delta^{13}C$)*

A separate data set was constructed of 32 observations, one for each of the 32 field-collected larvae whose isotope ratio was measured. The variables in this data set were the measured isotope ratio ($\delta^{13}C$) of each larva, the site in which it was collected, three of the four vegetation variables (grass cover, forb cover, and cover difference) of the subplot in which each larva was collected, and the $\delta^{13}C$ value expected under the null hypothesis of no selectivity in feeding (whose calculation is described above). The effects of each of the vegetation variables on isotope ratio was assessed with an analysis of covariance (ANCOVA) in which the dependent variable was larval isotope ratio and

the independent variables were site and the vegetation variable (covariate). Initially the interaction term (e.g., site x grass cover[cov]) was included in each analysis, but none of these interaction terms were significant, so the analyses were repeated without the interaction terms. The interaction terms in these analyses represent differences between sites in the slope of the line of isotope ratio against the vegetation variable; omitting an interaction term from an analysis is equivalent to assuming that the slopes are equal and so the sites differ only in the intercept.

*Comparison of observed and expected isotope ratios ($\delta^{13}C$)*

I used the same data set and ANCOVA to compare the 32 isotope ratios measured in field-collected larvae with the 32 corresponding values expected from the vegetation under the null hypothesis of no selectivity in diet (see above). In this analysis the dependent variable was the measured isotope ratio ($\delta^{13}C$) and the independent variables were site and expected $\delta^{13}C$ value (covariate). Because the interaction term (site x expected $\delta^{13}C$ value [cov]) was not significant, it was dropped from the analysis. Therefore the analysis in effect fitted five parallel lines, one per site, to the plot of observed $\delta^{13}C$ against expected $\delta^{13}C$ (Fig. 1.4). To quantify the degree of diet selectivity in each site, a new variable, the difference between measured $\delta^{13}C$ and expected $\delta^{13}C$, was calculated for each of the 32 larva. For each site separately, the mean value of this variable was compared with 0.0 using a t-test with an alpha-level of 0.01 (Bonferroni correction, to yield an overall alpha-level of 0.05).

## Results

### *White grub survey*

#### *Vegetation*

The mean total cover score of the 12 sites, calculated as described above on a scale of 0 to 4, was 3.9. No site had a mean total cover score less than 3.48. Mean grass cover score across sites (3.3) was much greater than mean forb cover score (1.7): these sites were dominated by grasses, in accordance with the site selection criteria (see above). The average difference between grass score and forb score, calculated as described above, was 1.6 (Fig. 1.2). However, Pace Bend Recreation Area had a more equitable cover of grasses and forbs, with a mean grass cover score of 2.3 and a mean forb cover score of 2.4.

Mean total cover score was positively correlated with mean grass cover score (Spearman's rank correlation coefficient, $r_s = 0.67$, $n = 12$, $P < 0.02$) but not with mean forb cover score. Mean grass cover score was negatively correlated with mean forb cover score (Spearman's rank correlation coefficient, $r_s = -0.80$, $n = 12$, $P < 0.002$).

#### *White grub density*

Density of white grubs was highly variable both within and among sites (Table 1.1). In general, medium-sized larvae were more abundant than small- and large-sized larvae. However at Pace Bend Recreation Area, which had many more larvae than any other site, most larvae were small. The number of larvae within a subplot (i.e soil core) was highly skewed with the large majority of subplots having no larvae and with relatively few subplots having more than one larva (Table 1.2).

*The relationship between white grub density and vegetation*

Across sites, there was a significant positive relationship between larval abundance and forb cover score (Spearman's rank correlation coefficient, $r_s = 0.73$, $n = 12$, $P = 0.007$) (Fig. 1.3). In contrast, there was a non-significant negative relationship between larval abundance and grass cover score (Spearman's rank correlation coefficient, $r_s = -0.53$, $n = 12$, $P = 0.08$). Larvae were less common at sites where there was a greater disparity between grass cover and forb cover (i.e. cover difference) (Spearman's rank correlation coefficient, $r_s = -0.66$, $n = 12$, $P = 0.02$).

***White grub $\delta^{13}C$ analyses***

*'Control' larvae*

Larvae fed exclusively a C4 plant diet *(Schizachyrium scoparium*, little bluestem grass roots) and a C3 plant diet (*Ipomoea batatas*, sweet potato), had $\delta^{13}C$ values (–16.0‰ and –24.6‰, respectively) that reflected their $C_4$ and $C_3$ diets, but these values did differ from the $\delta^{13}C$ values of their food sources, *S. scoparium* and sweet potato (–12.8‰ and –29.8‰, respectively) (Fig. 1.4).

*Effects of vegetation on isotope ratio ($\delta^{13}C$)*

There were significant effects of site and of two of the three vegetation variables (forb cover and cover difference) on larval $\delta^{13}C$ values (Table 1.3), but no significant interaction effects (see Methods). The $\delta^{13}C$ signature of larvae responded as expected to differences in vegetation cover (i.e., the direction of the slopes). $\delta^{13}C$ values were higher (less negative), though this was not significant (P = 0.06), in areas with greater grass cover and $\delta^{13}C$ values were significantly lower (more negative) in areas with greater forb

cover. Likewise, larval $\delta^{13}C$ values were significantly higher in areas with greater dominance of grasses to forbs (i.e., with greater cover difference).

*Comparison of observed and expected isotope ratios ($\delta^{13}C$)*

There was a significant positive relationship between measured $\delta^{13}C$ value and the $\delta^{13}C$ value expected from forb and grass cover under the null hypothesis of no diet selectivity, i.e., roots consumed in proportion to the relative cover of $C_3$ and $C_4$ plants (Table 1.3 and Fig. 1.4) (See Methods for a description of the calculation of these expected $\delta^{13}C$ values). Comparison of observed values and expected values (Fig. 1.5) indicated that only at Brackenridge Field Laboratory did the observed values significantly differ from those expected under the null hypothesis: the average observed $\delta^{13}C$ value of larvae at Brackenridge Field Lab was significantly lower (by 6.14‰) than the value expected under the null hypothesis (paired t-test comparing the differences between observed and expected values, df = 6 larvae, $P < 0.0001$; Bonferroni correction requires only $P < 0.01$ for an overall $P < 0.05$).

## Discussion

### *White grub survey*

*White grub density*

The density of white grubs (scarabaeid larvae) varied among sites from 0-55 $m^{-2}$ (Table 1.1). In general, root-feeding insects are usually aggregated and characterized as having a negative binomial distribution (Guppy and Harcourt 1970, Brown and Gange 1990). Because of the patchy distribution and the difficulty of locating larvae, very large samples are needed to obtain accurate density estimates. Therefore larval densities

reported here should be viewed cautiously. White grub densities reported from other grassland systems vary widely; most of them come from population outbreaks that resulted in an obvious reduction in aboveground foliage. For example, *Phyllophaga crinita* larvae, at a density of 46 $m^{-2}$, were associated with grass mortality in the Texas panhandle (Ueckert 1979). Larval densities of *Phyllophaga spp.* in Nebraska and Colorado from 11 $m^{-2}$ to over 200 $m^{-2}$ have been reported (Anonymous 1969, 1971a,b).

The differences in larval size at different sites suggest that the community composition of white grubs differed among these grassland areas. At the time of this survey (Feb-April), small larvae were most likely later stage larvae of a small-sized scarabaeid species rather than first instars of a larger scarabaeid species. Even small species of white grubs, such as black turfgrass ataenius (*Ataenius sp.*) can cause serious damage to plants at high density (Tashiro 1987). Only two of the medium-sized larvae were *Cyclocephala lurida* (southern masked chafer). All other medium-and large-sized larvae were second and third instars of *Phyllophaga spp.* (June beetles). The larvae of *Phyllophaga spp.* are the most common white grubs throughout the United States and are considered to be among the most destructive rangeland soil insects (Hewitt et al. 1974, Potter 1998).

The observed densities in this study likely represent low estimates of larval abundance, since larval abundance is lowest during the time of year at which this survey was conducted (Feb-April), i.e., shortly before pupation in the spring (Teetes et al. 1976). In addition, prior to this survey the region experienced several years with periods of exceptionally hot and dry weather. Many of these events occurred during the time of adult flight (May-June) and larval feeding development (June-September) and likely resulted in subsequent years of low reproduction and low larval survival. Indeed, Brown and Gange (1990) note that soil moisture is probably the single most important factor in the abundance of soil insects. In several sites, including Hamilton Pool Nature Preserve where I found no white grubs, I did find un-hatched eggs (presumably those of white

grubs), perhaps due to insufficient soil moisture for development (Gaylor and Frankie 1979, Potter 1983).

*Other factors affecting abundance - soil texture*

Differences in soil moisture among sites associated with soil texture and variation in precipitation may have important consequences for larval mobility and survival (Turpin and Peters 1971, Gaylor and Frankie 1979, Stone and Bueno 1987, Katovich et al. 1998). For instance, *Popillia japonica* (Japanese beetle, Scarabaeidae) egg development and first instar survival were higher in finer textured soils due to their greater water holding capacity (Régniere et al. 1981). However, Stone and Bueno (1987) found that larval vertical migration improved in coarser soils, and that soil texture had no effect on survival. Improved migration ability better enables larvae to adjust to changes soil moisture and temperature (Fleming 1972, Bueno et al. 1988). In this study, soils did vary among sites (see Appendix A), but there was no clear relationship with white grub density. For example, among the three sites with higher grub densities, Pace Bend Recreation Area had the coarsest (i.e., sandiest) soils of all sites while Brackenridge Field Lab and Shield Ranch-ungrazed had finer clay soils. Different species of white grubs may also be more prevalent in different soil conditions (Katovich et al. 1998). In areas with highly variable precipitation and frequent drought, there may be a tradeoff for oviposition between soils with greater water holding capacity and soils that allow larval mobility, and therefore allow larvae to tolerate or adjust to changing environmental conditions.

*Other factors affecting abundance - predation / parasitism*

White grubs are known to have a variety of parasites and predators, although their impact on white grub abundance in natural systems is lacking. In New Zealand, the

decline in density of scarabaeid larvae (*Costelytra zealandica*) in older-aged pastures was attributed to the increased abundance of bacterial and fungal pathogens (East and Willoughby 1983). Parasitic microorganisms of *Phyllophaga spp*. larvae in the United States include milky disease bacteria (*Bacillus spp*.), fungi (e.g., *Cordyceps ravenelii*, *Metarrhizium anisopliae*), and nematodes. Several fly species (Family Asilidae) and wasp species (Family Tiphiidae) are also known parasites of *Phyllophaga* larvae and pupae (Tashiro 1987). None of the larvae that I collected showed signs of parasitism, but I did find cocoons of tiphiid wasps at several sites. Mammalian predators include skunks, raccoons and armadillos (Potter 1998). The red imported fire ant (*Solenopsis invicta*) may also be a significant direct source of white grub mortality (S. Brumbaugh, personal observation). The invasion of *S. invicta* into areas is often accompanied by a decrease in the local aboveground fauna (Porter and Savignano 1990) and it may be having a similar effect on the belowground fauna. Overall, the factors affecting white grub abundance in grassland and savannas are likely complex due to the interaction of abiotic (e.g. soil type, precipitation) and biotic (e.g. vegetation, predators/pathogens) conditions.

*Other factors affecting abundance – land use*

Regional land-use patterns can also influence the spatial distribution and abundance of white grubs. Several of the grassland sites in this study were located in or near urbanized and developed areas (Fig. 1.1). Because adult beetles are attracted to lights (Potter 1998), and because well-watered lawns and golf courses can support large populations of white grubs (Tashiro 1987), proximity to these areas may affect white grub population and community dynamics in grasslands. However, it is uncertain whether these areas would serve as population sources or act as population sinks by attracting adult beetles away from surrounding grassland sites. Brackenridge Field Lab, the most urban site that I surveyed, was also near a golf course which may have been a factor in the relatively high white grub abundance at this site.

Many study sites were situated in or near areas that have been heavily grazed. Several studies have found that intense aboveground herbivory can negatively impact populations of root herbivore through the concomitant reduction of root tissue. However, there are other examples where white grub populations increased with moderate intensity grazing (Hutchinson and King 1980) and mowing (Seastedt 1985). Livestock may also negatively affect white grub populations by altering soil conditions (e.g. compaction, moisture content, and temperature) associated with trampling and reduced plant biomass. Of the two Shield Ranch sites, the ungrazed site had considerably higher white grub abundance than the grazed site at Chalk Hill. However, white grub densities at other rural ungrazed sites (e.g. Gloster Bend Recreation Area and Hamilton Pool Nature Preserve) were extremely low, so the effect of grazing history is not clear.

*White grub association with vegetation*

White grubs are known primarily as pest species of grasses in a variety of grass-dominated systems (e.g., rangelands, pastures, crops, and lawns) (Graber et al. 1931, Schumacher 1959, Teetes 1973, Ueckert 1979, Merchant and Crocker 1995, Rodriguez del Bosque 1995, Coffin et al. 1998, Potter 1998). Therefore, my discovery of greater abundances of white grubs in sites with greater forb presence and lower abundances in areas with greater grass dominance (Fig. 1.3) was not expected. The possibility that higher grub densities resulted in the greater forb and lesser grass presence (see Ueckert 1979 and Coffin et al. 1998 for examples) in the study sites cannot be dismissed. However, it seems unlikely that grubs could have had such an impact at the relatively low densities at most sites.

Because of the low mobility of soil insects (Andersen 1987), the distribution and abundance of white grubs ultimately depends on oviposition selection. *Phyllophaga crinita*, the most common and destructive white grub species in Texas and northern Mexico (Drees and Jackman 1998, Potter 1998), is known to preferentially oviposit in

fields sown with grasses (e.g. sorghum and corn) over those with beans (Rodriguez del Bosque 1984). Yet, in natural systems open sites that are colonized by forbs may also provide greater ovipositing access to the soil. Therefore the higher densities of larvae where forb cover was greater could be a consequence of selective oviposition.

***White grub $\delta^{13}C$ analyses***

*'Control' larvae*

The $\delta^{13}C$ signature of 'control' larvae fed only a $C_4$ or a $C_3$ diet reflected the $\delta^{13}C$ differences of their respective food plants, but larval $\delta^{13}C$ values differed from the $\delta^{13}C$ values of their food items more than expected (Fig. 1.4). Larval $\delta^{13}C$ signatures may have been influenced by the diet of first instars prior to collection. First instars were collected an area dominated by a $C_4$ grass and this may account for the fact that larvae fed a $C_3$ diet had higher $\delta^{13}C$ values than their food. Greater water-use efficiency of plants can also result in enriched $\delta^{13}C$ values (Farquhar and Richards 1984, Farquhar et al. 1989b). It is possible that the greenhouse *Schizachyrium* plants eaten by 'control' larvae were less water stressed, and therefore had lower water-use efficiency, than the *Schizachyrium* plant used for isotope analysis, which was grown outdoors. The deviations in the isotope signatures between larvae and the different food items suggests that the isotopic response of these organisms was more sensitive to growing conditions than expected. Therefore, I plan on conducting additional stable carbon isotope analyses on larvae reared from eggs, analyzing the isotopic signature of each larvae along with the specific $C_4$ or $C_3$ plant fed to each larva.

*Effects of vegetation on isotope ratio ($\delta^{13}C$)*

The $\delta^{13}C$ values of *Phyllophaga* larvae collected in central Texas indicated that the dietary contribution of grasses and forbs differed among sites (Table 1.3). The lower than expected $\delta^{13}C$ values of larvae at BFL indicated that larvae at this site were selectively feeding on $C_3$ forbs over the $C_4$ grasses (Figs. 4 and 5). This was contrary to my hypothesis that white grubs selectively fed on grasses over forbs.

The variation among sites in the degree to which larvae fed selectively may by explained by several factors. Root abundances were assumed to be closely related to cover score. Sources of error therefore include differences between cover score and actual cover, between cover and aboveground biomass, and between aboveground biomass and root abundance. For example, root:shoot ratios may differ among species and between plant functional types (Cahill 2003, Müller et al. 2000). Root:shoot ratio can also vary with plant size or resource availability (Chapin 1980, Wilson 1988, Cahill 2003). Differences among sites in feeding selectivity may also have been caused by differences among sites in the *Phyllophaga* species present. Finally, differences among sites in forb community composition may have caused the differences in feeding selectivity among sites. In general, dicot species can vary considerably in their palatability to herbivores due to nutritional content (i.e., C:N) and the diversity of secondary metabolism (Rhodes and Cates 1976, Coley et al. 1985, Coley and Barone 1996). Grasses, in contrast, often have higher C:N content than forbs and generally lack sufficient chemical defenses to deter herbivores (McNaughton 1983, Moles and Joern 1993). Therefore, in sites with a greater presence of toxic or unpalatable forb species white grubs may selectively feed on grasses, but they may selectively feed on forbs in sites with more palatable forb species. The study of plant secondary chemistry and plant-herbivore interactions belowground has received little attention (Karban and Baldwin 1997), but remains an important topic in understanding the effects of root herbivores on plant community structure and dynamics (Van der Putten 2003).

In conclusion, this study is a descriptive survey of white grub abundance and diet in 12 grassland and savanna sites in central Texas. White grub abundance was closely related to the relative abundance of grasses over forbs. If this was due to differential oviposition, rather than to a direct effect of grubs on plant community composition, it suggests that these grubs have a greater negative effect on forbs than grasses in these grassland and savanna communities. Other studies have found that belowground insect herbivores can accelerate plant succession by suppressing forb species, thereby enhancing the colonization and production of late seral grasses (Brown and Gange 1989b, 1992, Schädler et al. 2004). However, several studies have shown that white grubs have a greater effect on grasses than on forbs (Ueckert 1979, Coffin et al. 1989). The variation among sites independent of vegetation composition is less easily interpreted. Only in one site was there evidence that grubs were feeding selectively; in that site they preferentially fed on forbs. This may reflect the particular forb species or grub species present in that site. Overall, these results suggest that the effect of white grubs on plant species composition in these, and possibly other grasslands and savannas, is influenced strongly by a combination of local biotic and abiotic factors, and in turn may contribute to vegetation heterogeneity at the landscape level.

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Table 1.1. Mean density (± 1 SE) of white grubs per $m^2$ at 12 sites in central Texas. The different larval size classes are: small (< 0.15 g), medium (0.15-0.50 g), and large (> 0.50 g). Approximately 40% of larvae could not be weighed due to damage during soil excavation. The size class of each damaged larva was estimated visually.

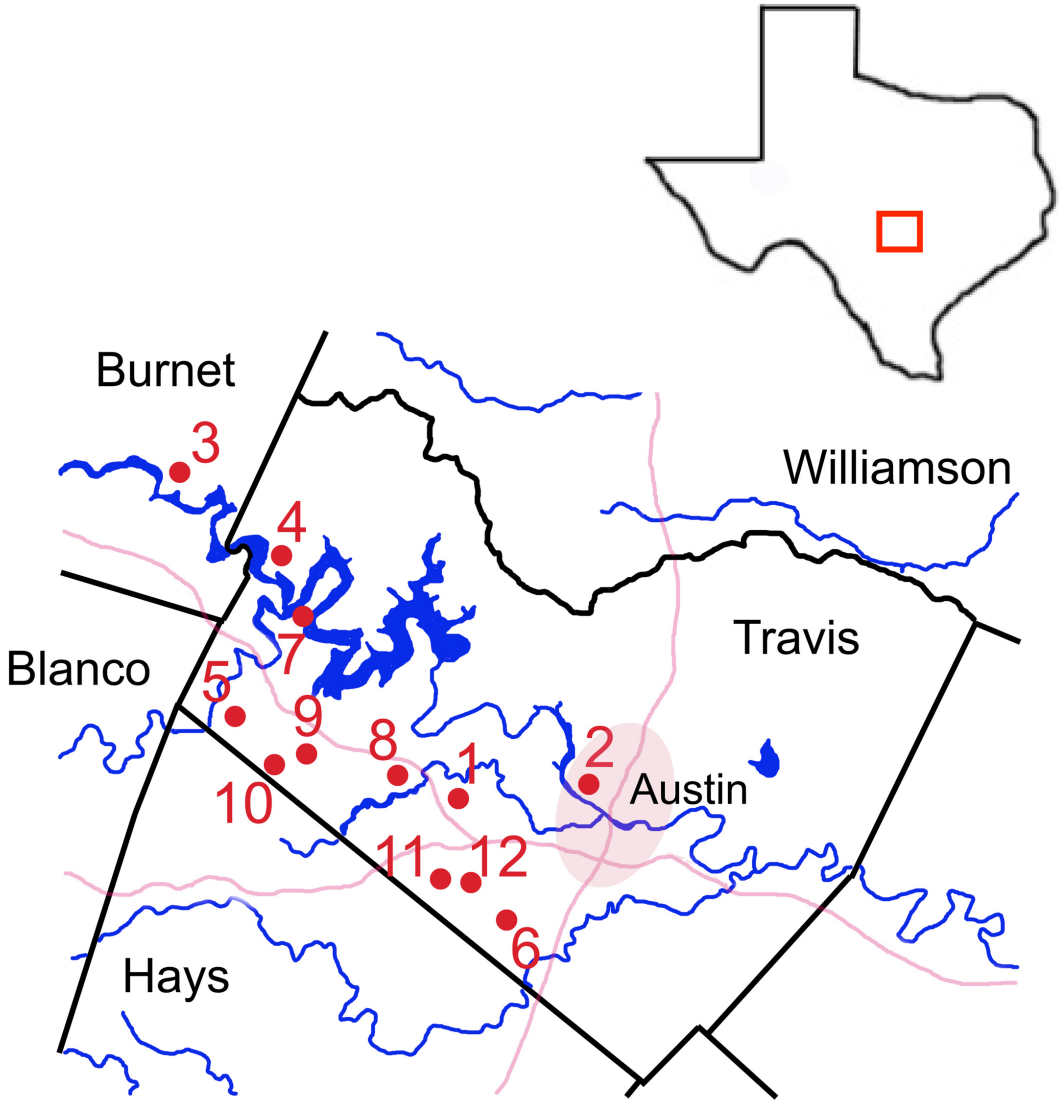
| | | | Larval size class | | | | | |
|---|---|---|---|---|---|---|---|---|
| | All larvae | | Small | | Medium | | Large | |
| Site | Mean | (SE) | Mean | (SE) | Mean | (SE) | Mean | (SE) |
| Barton Creek Nat. Preserve | 10.19 | (4.87) | 4.53 | (2.77) | 5.66 | (3.10) | 0 | |
| Brackenridge Field Lab | 22.64 | (4.73) | 4.53 | (2.12) | 5.66 | (2.53) | 12.45 | (4.16) |
| Camp Creek Rec Area | 12.45 | (3.30) | 10.19 | (2.12) | 1.13 | (1.31) | 1.13 | (1.31) |
| Gloster Bend Rec Area | 4.53 | (4.53) | 0 | | 4.53 | (4.53) | 0 | |
| Hamilton Pool Nat. Preserve | 0 | | 0 | | 0 | | 0 | |
| LBJ Wildflower Center | 15.84 | (7.02) | 4.53 | (2.12) | 10.19 | (4.53) | 1.13 | (1.13) |
| Pace Bend Rec. Area | 55.46 | (10.80) | 39.61 | (10.74) | 10.19 | (2.77) | 5.66 | (3.10) |
| Porter Ranch | 7.92 | (2.26) | 2.26 | (1.39) | 5.66 | (1.79) | 0 | |
| Shield Ranch-Chalk Hill | 7.92 | (3.84) | 5.66 | (3.10) | 1.13 | (1.13) | 1.13 | (1.13) |
| Shield Ranch-ungrazed | 26.03 | (8.88) | 2.26 | (2.26) | 20.37 | (8.112) | 3.40 | (1.39) |
| Slaughter Tract | 14.71 | (4.60) | 1.13 | (1.13) | 10.19 | (5.19) | 3.40 | (1.39) |
| Slaughter cemetery | 9.05 | (2.89) | 1.13 | (1.13) | 6.79 | (2.12) | 1.13 | (1.13) |

Table 1.2. Number of soil cores (one per subplot) with *n* larvae. A total of 165 larvae was found in 600 soil cores pooling all 12 sites. The total surface area of soil cores was 176.6 $cm^2$.

| Number of larvae per soil core | Number of soil cores |
|---|---|
| 0 | 482 |
| 1 | 83 |
| 2 | 27 |
| 3 | 6 |
| 4 | 1 |
| 5 | 0 |
| 6 | 1 |

Table 1.3. ANCOVA results for $\delta^{13}C$ values of larvae among five grassland-savanna sites in central Texas. Separate analyses were done using grass cover, forb cover, cover difference (grass cover - forb cover), and expected $\delta^{13}C$ values of larvae as covariates.

| *Source of Variation* | *d.f.* | *SS* | *F-value* | *P-value* | *slope* |
|---|---|---|---|---|---|
| site | 4 | 102.95 | 4.65 | <0.01 | |
| covariate (grass cover) | 1 | 21.67 | 3.92 | 0.06 | 1.05 |
| error | 26 | 143.91 | | | |
| site | 4 | 102.95 | 5.37 | <0.01 | |
| covariate (forb cover) | 1 | 41.10 | 8.57 | <0.01 | -1.36 |
| error | 26 | 124.52 | | | |
| site | 4 | 102.96 | 5.12 | <0.01 | |
| covariate (cover difference) | 1 | 34.82 | 6.92 | 0.01 | 0.69 |
| error | 26 | 130.76 | | | |
| site | 4 | 102.95 | 5.06 | <0.01 | |
| covariate (expected $\delta^{13}C$) | 1 | 33.42 | 6.58 | 0.02 | 0.35 |
| error | 26 | 132.16 | | | |




1. Barton Creek Nature Preserve
2. Brackenridge Field Laboratory
3. Camp Creek Recreation Area
4. Gloster Bend Recreation Area
5. Hamilton Pool Nature Preserve
6. Lady Bird Johnson Wildflower Center
7. Pace Bend Recreation Area
8. Porter Ranch
9. Shield Ranch – Chalk Hill
10. Shield Ranch – Ungrazed
11. Slaughter Tract
12. Slaughter - Cemetery

Figure 1.1. Location of survey sites in central Texas. All sites are located on the eastern Edwards Plateau in Travis and Burnet Counties.

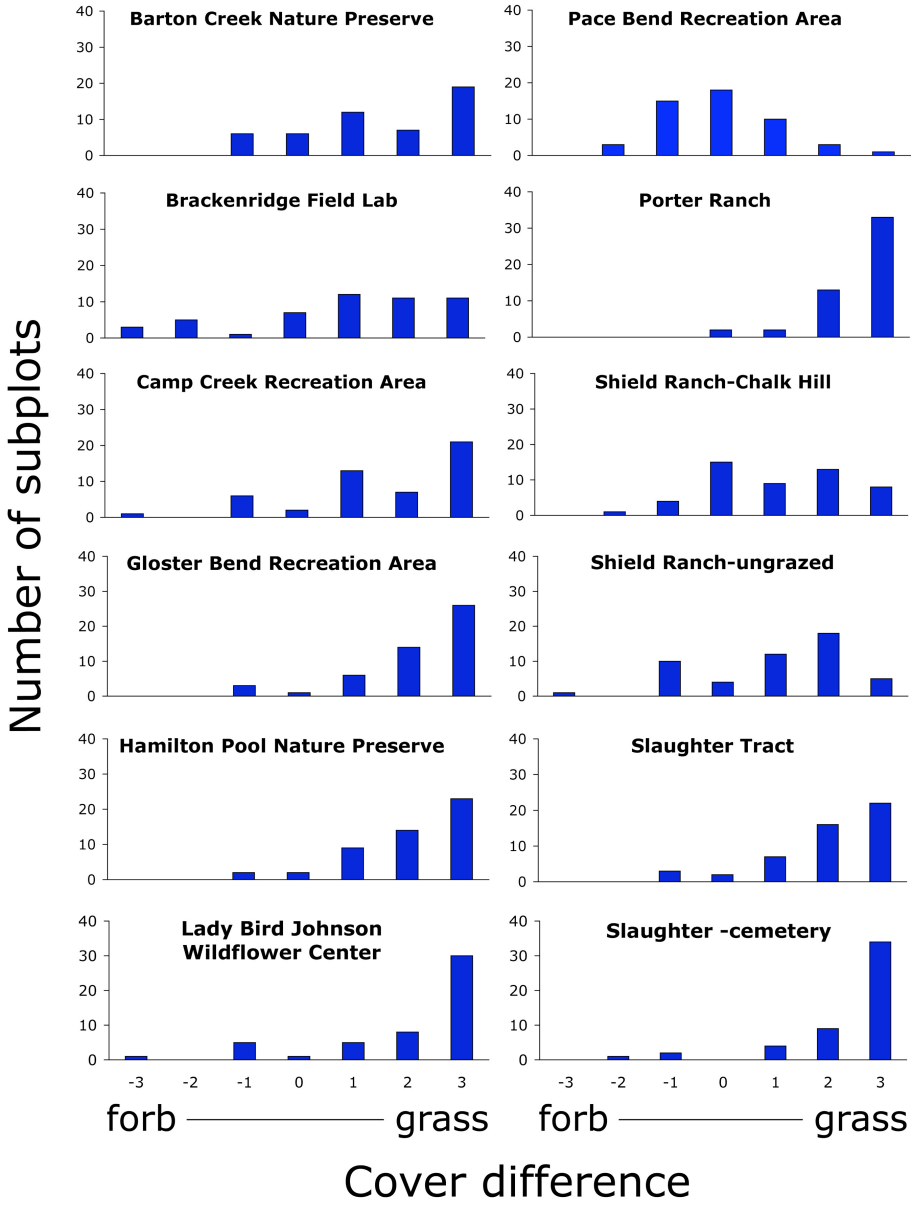



Figure 1.2. Cover difference of grasses and forbs at 12 sites in central Texas. N=50 subplots at each site. Cover difference = grass cover score - forb cover score. A positive cover difference means that the subplot had a higher grass cover score than forb cover score; a negative cover difference means that the subplot had a higher forb cover score than grass cover score. Cover scores were based on absolute percent cover: 1 = 0-25%, 2 = 25-50%, 3 = 50-75%, and 4 = 75-100%.

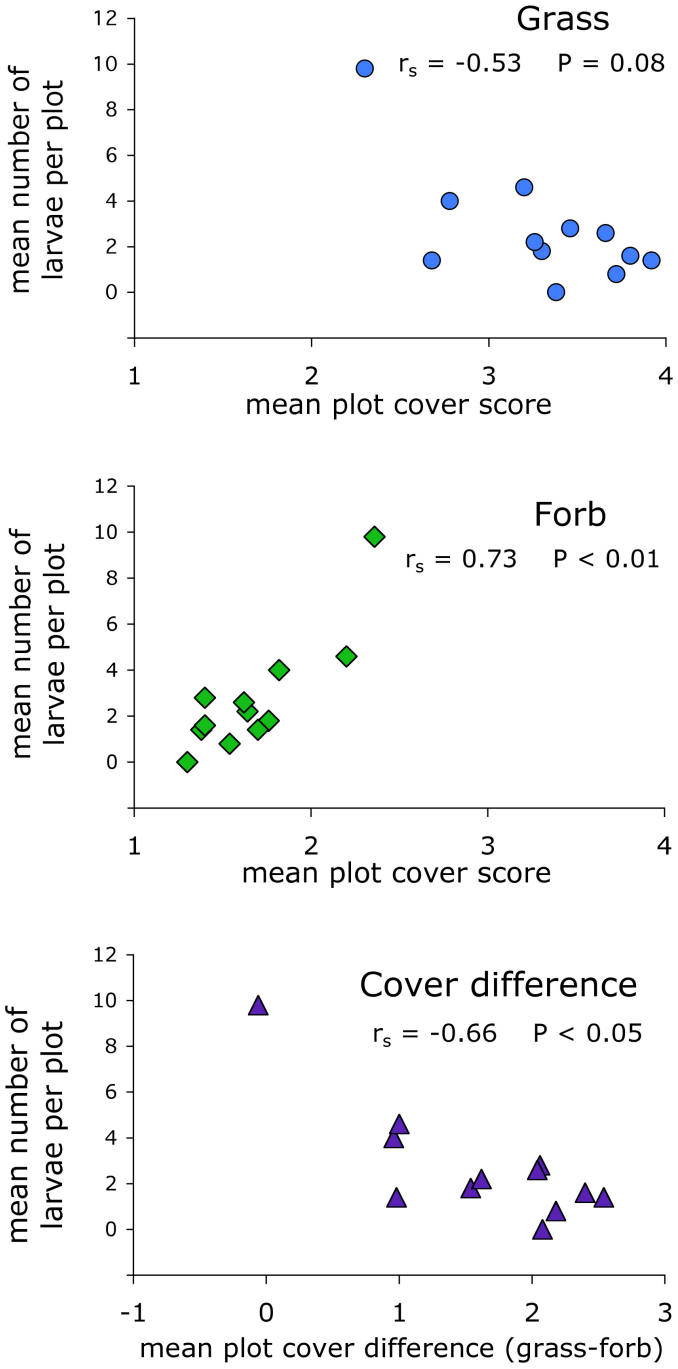



Figure 1.3. Relationship of mean number of larvae per plot with the mean plot cover score for grass, forb, and cover difference (grass cover - forb cover) at the 12 sites. $r_s$, Spearman's nonparametric correlation coefficient.

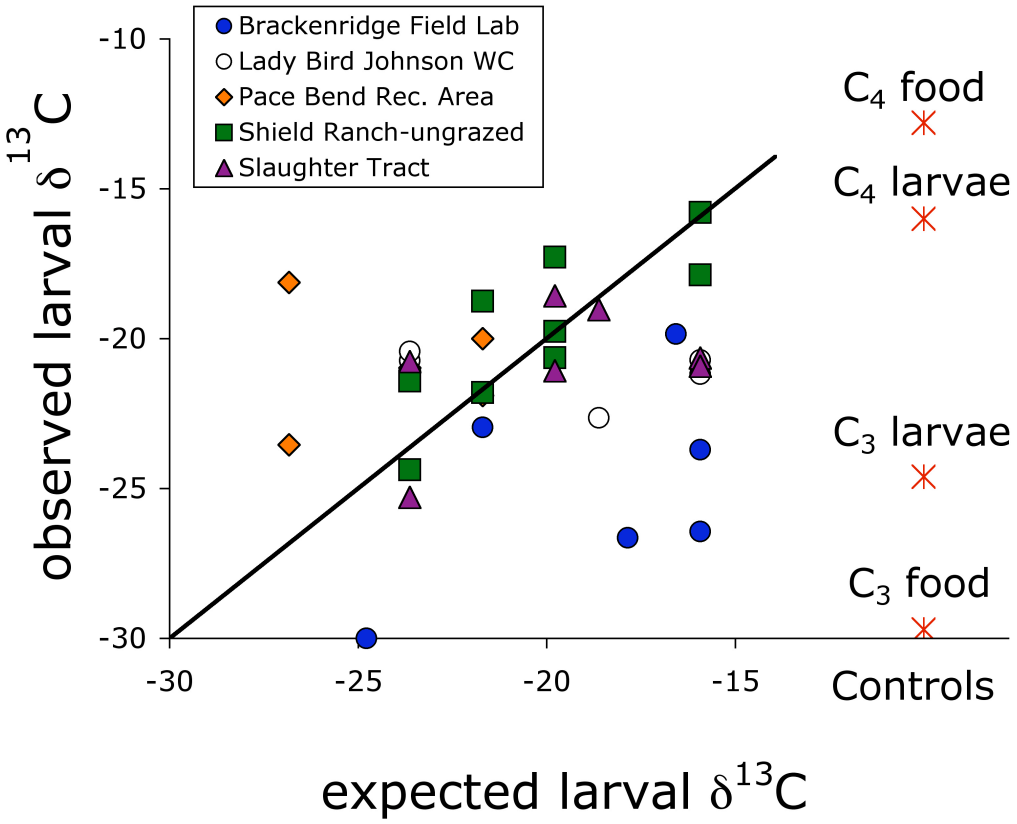



Figure 1.4. Observed and expected $\delta^{13}C$ values of larvae at five grassland sites in central Texas. Expected values from the null hypothesis of no selectivity in diet are represented by the line. Values above and below the line indicate preferential feeding on $C_4$ and $C_3$ plants, respectively. $C_3$ larvae: $\delta^{13}C$ values of larvae fed a $C_3$ (sweet potato) diet; $C_4$ larvae: $\delta^{13}C$ values of larvae fed a C4 (*S. scoparium* roots) diet; $C_3$ food: $\delta^{13}C$ values of sweet potato; $C_4$ food: $\delta^{13}C$ values of *S. scoparium* roots.

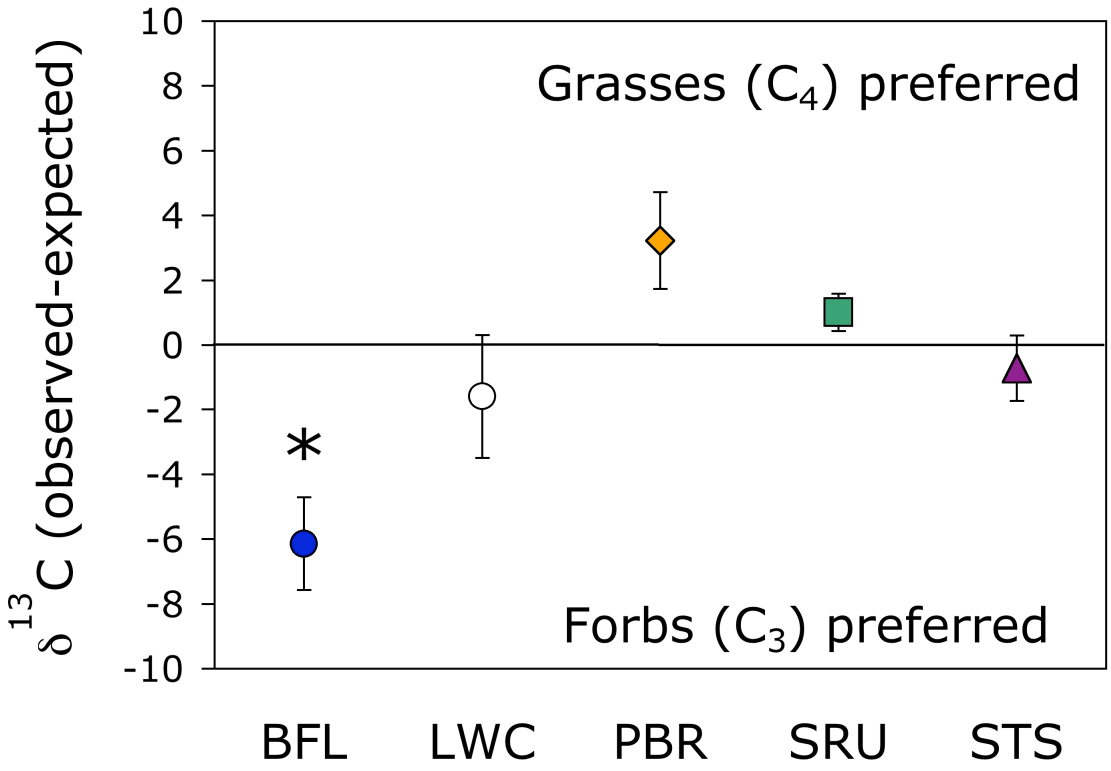



Figure 1.5. Mean (± 1 SE) difference between observed and estimated $\delta^{13}C$ values of larvae at five grassland-savanna sites in central Texas. Sites are Brackenridge Field Lab (BFL), Lady Bird Johnson Wildflower Center (LWC), Pace Bend Recreation Area (PBR), Shield Ranch-ungrazed (SRU), and Slaughter Tract (STS). Values above and below the line ($\delta^{13}C=0$) indicate a feeding preference for $C_4$ grasses and $C_3$ forbs, respectively. The mean $\delta^{13}C$ value at BFL differs significantly from the null expectation of 0 (t-test with an adjusted significance level using the Bonferroni method, n = 6, $P < 0.008$).

# Chapter 2 - Selective root herbivory by *Phyllophaga crinita* Bur. (Coleoptera: Scarabaeidae) larvae for common co-occurring plants in Texas savannas.

## Introduction

The selective feeding of herbivores can have important impacts on individual plant performance (i.e., survival, fecundity, growth, competitive ability) and on plant populations, which in turn can affect community structure and ecosystem processes (Harper 1977, Crawley 1983, Brown and Heske 1990, Huntley 1991, Louda et al. 1990, Olff and Ritchie 1998). In grasslands and savannas, the reduction of grass production by intense livestock grazing is believed to be a key factor in the increase in woody plant cover and abundance (Archer 1994). However, in these systems, the majority of net primary production and plant biomass is commonly allocated to belowground structures (Coleman 1976, Sims and Singh 1978, Jackson et al. 1996) and competition for water is a central component of grass-woody plant interactions (Fowler 1986, Scholes and Archer 1997, Van Auken 2000). Furthermore, invertebrate root herbivores in grasslands may consume nearly twice as much plant biomass as cattle grazing (Smolik et al. 1976, Scott et al. 1979). Nevertheless, we have a poor understanding of plant-herbivore interactions that occur underground and how these interactions influence plant communities (reviewed in Andersen 1987, Brown and Gange 1990, Mortimer et al. 1999, Hunter 2001). This study examines the feeding behavior of a common insect root herbivore and its effect on a dominant native grass in many Texas grasslands and savannas. For simplicity, I use the term "root herbivory" broadly to refer to the consumption of plant tissues that reside underground.

Several studies have shown that belowground herbivores can alter rates of succession by suppressing either the dominant grass species (Ueckert 1979, Coffin et al. 1998, Seabloom and Richards 2003) or subordinate forbs species (Brown and Gange

1989, 1992), presumably by differential feeding. There are few, if any, studies that examine the effect of insect root herbivores on woody plant performance in grasslands and savannas (but see Fowler and Wilson 1971, Karban 1980, and Maron 2001 for examples in non-grass dominated systems). Because of the difficulty in observing the activities of organisms residing underground, the effect of subterranean herbivory may often go unnoticed or attributed to other factors, such as abiotic stress or competition (Hewitt et al. 1974, Connell 1990). Even when we know that root herbivores are present, their feeding behavior is often inferred only from changes in aboveground foliage.

This study examines the feeding preferences of a common insect root herbivore for four co-occurring plant species and its effects on these plant species. I observed the feeding behavior of *Phyllophaga crinita* Burmeister (May or June beetle) larvae (commonly called white grubs) in a two-choice environment pairing a native dominant bunchgrass, *Schizachyrium scoparium* (Michx.) Nash (little bluestem), with three invasive plant species: *Bothriochloa ischaemum* [L.] Keng. (King Ranch bluestem grass), *Prosopis glandulosa* Torr. (honey mesquite), and *Juniperus ashei* Bucholz (Ashe juniper). *B. ischaemum* is an exotic bunchgrass that has supplanted many native grasses (Gabbard 2003); *P. glandulosa* and *J. ashei* are native woody plants and are considered invasive due to their increasing abundance in grasslands and savannas (Archer 1994). All four plant species commonly co-occur in savannas in central Texas.

Subterranean observation windows (rhizotrons) and tubes (mini-rhizotrons) are commonly used for the study of plant root systems (Böhm 1979). However, these methods, which typically require the opportunistic encounter of organisms with the observation window, do not allow the continuous observation of mobile animals. To observe the daily feeding behavior of *P. crinita* larvae, I used thin (1.5-2.0 cm) transparent pots, as two-sided rhizotrons that allowed me to view larval location and feeding activity, as well as plant root systems. I addressed the following questions: 1) do *P. crinita* larvae demonstrate a preference between the dominant native grass, *Schizachyrium scoparium*, and the three invasive species, and if so, is there evidence for

selective feeding between plant functional types (i.e. grasses or woody plants), and 2) is *Schizachyrium scoparium* performance affected by larval feeding?

For this study, I use a definition of 'preference' similar to Hassell and Southwood (1978) and Crawley (1983), who define preference as a non-random pattern of feeding such that the proportional consumption of a food item is different than the relative abundance of that item in the available habitat (but see Miller and Stickler 1984, Singer 1986, 2000, for other definitions). In this study larvae are presented with two food choices in similar proportions. Because of the difficulty in quantifying the consumption of roots by larvae, I use the amount of time that larvae were associated with a particular plant and their position in the pot as surrogates for root consumption. I use this consumption-based definition of preference typically used by ecologists (Singer 1986) because it emphasizes the differential damage to plants caused by selective feeding, and thereby the potential consequences for plant community dynamics.

*Phyllophaga crinita life history*

*Phyllophaga spp*. (May and June beetles) (Coleoptera: Scarabaeidae) larvae feed on the roots of a variety of plants and are considered to be among the most destructive soil insects in grasslands (Hewitt et al. 1974). *Phyllophaga crinita* is the most common species of June beetle in Texas (Potter 1998) and is reported to cause damage to rangelands (Ueckert 1979), turfgrass (Merchant and Crocker 1995), and a variety of grass crops (Teetes 1973, Huffman and Harding 1980, Rodriquez del Bosque 1996). *P. crinita* has a one-year life cycle except in the northern limits of its range (north Texas to Oklahoma) where the life cycle can be two years. The adults emerge from the ground and take flight during late spring or early summer, usually a few days after rainfall events (Gaylor and Frankie 1979). Within a few days of emerging, the females oviposit 20-50 eggs within the top 10 cm of soil. Eggs typically hatch within three to four weeks. Larvae become third instars, the final and main feeding stage, by late summer or early

fall and they continue feeding until the onset of cold weather, at which time they move deeper in the soil and overwinter (Potter 1998).

## Methods

*Pot and experimental design*

I conducted this experiment in a greenhouse at the University of Texas at Austin, Austin, TX. To observe *Phyllophaga crinita* Bur. larval feeding activity and plant root systems, I constructed thin transparent pots (Fig. 2.1) that created a two-choice feeding environment pairing *Schizachyrium scoparium* (Michx.) Nash (little bluestem grass) with each of three other plant species: *Bothriochloa ischaemum* (L.) Keng. (King Ranch bluestem grass), *Prosopis glandulosa* Torr. (honey mesquite), and *Juniperus ashei* Buchh. (Ashe juniper). I transplanted individuals of all four plant species (see details below for plant rearing and transplanting) separately into thin, square clear acrylic pots (30 cm high x 30 cm wide x 1.5 cm thick) that were covered with an adhesive paper to prevent light penetration. Just prior to the beginning of the feeding trial, the adhesive paper was removed, one 30 cm high x 1.5 cm thick side was removed from each pot, and pairs of pots were taped together, making a new pot 30 cm high x 60 cm x 1 cm thick (Fig. 2.1). Each new pot had one *P. crinita* plant and one individual of another species: *P. glandulosa*, *J. ashei*, or *B. ischaemum*. There were 30 pots per plant combination, 90 in all. To prevent roots from one plant crossing over to the other side of the pot, I opened pots weekly and ran a razor blade along the seam connecting the two pot sides. I also covered the pot sides with black plastic to minimize the exposure to light. During the experiment and at the time of plant harvesting, there was no evidence of roots crossing pot sides.

On 8 Oct., 2001, a single larva was placed 2-cm deep and equidistant from the two plants in each pot. To evaluate the effect of larval feeding on *Schizachyrium*

*scoparium* growth, I also grew six grasses individually in half-sized pots (i.e., 30 x 30 cm pots without adjoining neighbors) without larvae. I placed each of the pots (15 full-sized pots with larvae plus one half pot without a larva per frame) in one of six box frames that were placed in two rows of three on the greenhouse table. I turned each pot 180° and placed it in an adjacent box frame every day. I mapped larval location daily for 59 days between noon and 3 p.m. If larval location in the pot did not change for four or more days, all those days were considered to be 'inactive days' and were dropped from the data set. If a larva had <40 active days due to mortality or early feeding dormancy, I dropped all observations of that larva from the data set. This resulted in 8-11 pots being omitted for each plant combination treatment. In most pots, there were several days on which larvae could not be seen. If I observed larvae on the same side of the pot before and after the day(s) they could not be seen, I assumed that they spent the intervening day(s) on that side of the pot. If larvae were seen on the other side of the pot after the missing day(s), I assumed that they changed sides once in the middle of the time period during which they were not visible. Most missing observations lasted only a single day, and none of these periods was longer than three days.

From these observations of larval location, I calculated three measures of larval food preference for each larva: (1) the proportion of its active days that it spent on the *S. scoparium* side of its pot, (2) its average distance from the pot center (pot center being defined as the seam between the two joined half pots), and (3) the average length of its feeding bouts. I defined a feeding bout as a set of consecutive days during which a larva remained on the same side of the pot, so for each larva an average *S. scoparium* feeding bout length was calculated along with an average feeding bout length on the other plant species in the pot. At the completion of the study, *S. scoparium* plants had soil washed from the roots and were dried at approximately 65°C. I cut roots where they joined the wood-like basal crown and weighed shoot (green tillers and basal crown) and root tissues separately. I calculated *S. scoparium* root:shoot ratios as root mass divided by shoot mass.

*Plant rearing*

*Prosopis glandulosa*, *Juniperus ashei*, and *Bothriochloa ischaemum* were grown in pots (6 cm diam. x 25 cm deep) containing 1:1 Scotts Metro Mix 700™ potting medium and sand. I grew *Prosopis* plants from seeds collected in Travis Co., Texas. Seeds were germinated in January 1999 by lightly scarifying the seed coat and then soaking the seeds in water. *Juniperus* individuals (approx. 10-15 cm tall) were collected in February 1999 at Brackenridge Field Laboratory (BFL), Austin, Texas. Root systems of these plants were largely intact to approximately 10 cm in depth. Soil was washed from the roots before transplanting individuals into pots in the greenhouse. In February 2001, I grew *Bothriochloa* plants from seed collected in Blanco Co., TX. Seeds were sown in flats and new germinants were transferred to pots. I watered all plants as needed (approximately twice a week) and fertilized (Scotts Peters Professional fertilizer™ [20-10-20]) approximately every 2-3 months until they were transplanted into experimental pots.

In early June 2001, I separated sets of 3-5 tillers of *Schizachyrium scoparium* plants collected in Travis Co., TX. Soil was washed from the roots of each set of tillers (i.e., experimental plant) before planting them into experimental half-sized pots (30 x 30 cm). The other three species were transplanted into experimental half-sized pots in early August 2001. I transplanted all plants into the center of the half-sized pots. Experimental pots contained soil consisting of 1:1 sandy loam and sand; the sandy loam was collected at Brackenridge Field Laboratory (BFL), Austin, TX, and was sifted to remove all noticeable plant material. Following transplanting, I watered all plants twice a week. For the first two weeks, fertilizer (Earth Safe Organics™ seaweed extract) was used to stimulate root growth. At the beginning of the feeding trial, all plants had fine roots throughout their half of the pot.

*Larval rearing*

I captured *Phyllophaga crinita* adults April-June 2001 at BFL using trap lights. I placed males and females together in containers with 10-15 cm moist sand (approximately 10-15% gravimetric soil moisture) for ovipositing and egg hatching. Newly hatched first instar larvae appeared approximately three weeks following adult capture. I kept individual first instars in small cups containing moist sand and I fed them pieces of sweet potato. For feeding trials, I used only third instar larvae.

*Statistical Analyses*

I performed statistical analyses on larval preference measures using S-Plus Standard (Insightful Corp., Seattle, Washington, USA). I used SAS v8.0 (SAS Institute 1999) for statistical analyses of *S. scoparium* biomass measures. I tested the proportion of total active days that each grub spent on the side of *S. scoparium* against the null distribution (where $\mu=0.5$) using a one-sample t-test. Proportions were arcsine transformed for analysis and then back transformed for reporting. To determine whether larvae changed their plant preference during their active period, I used a paired t-test for each plant combination to compare the proportion of time that each larva spent on *S. scoparium* in the first half with the second half of the larva's active period. I used a one-sample t-test to test the mean horizontal location of larvae against the null distribution (where $\mu=0$) for each plant combination. Only observed locations were used for this analysis (i.e., missing days were not estimated). For each of the plant species pairs, I used a paired t-test to test the difference in mean feeding bout duration of each larva on *S. scoparium* and on the neighboring plant. Differences in *S. scoparium* total biomass and root:shoot mass ratio were tested using single factor analysis of variance (ANOVA). Pair-wise differences between means were performed using Tukey's *a posteriori* multiple comparison method.

## Results

### *Phyllophaga crinita feeding preference*

On average, the *Phyllophaga crinita* larvae in pots with *S. scoparium and J. ashei* spent 70% of their active days on the *S. scoparium* side of their pots, a value significantly greater than the null expectation of 50% (one-sample t-test on arcsine transformed data, $P < 0.0001$) (Fig. 2.2). There was also a non-significant trend ($P < 0.11$) for larvae in pots with *P. glandulosa* to spend more time on the *S. scoparium* side of those pots. There was no difference statistically in the average time that each larva spent on the *S. scoparium* pot side between the first and second half of each larva's total active period for any of the three plant species pairs (by paired t-tests comparing the mean proportion of active days on the *P. crinita* side in each time period) (Fig. 2.3).

On average, larvae in pots with *J. ashei* were located 5.8 cm from the pot center on the *S. scoparium* side of the pot ($P < 0.0001$, one-sample t-test, against a null hypothesis of 0 cm) (Fig. 2.4). Larvae in pots with *P. glandulosa* were on average located 2.3 cm from the center on the S. scoparium side of the pot, although this was not significantly different from 0 cm ($P = 0.06$, one-sample t-test).

In pots with *S. scoparium* and *J. ashei*, feeding bouts on *S. scoparium* were on average more than twice as long as feeding bouts on *J. ashei* (16.7 days versus 6.6 days, $P < 0.0001$, paired t-test) (Fig. 2.5). There were no significant differences in average feeding bout length between *S. scoparium* and *P. glandulosa* or between *S. scoparium* and *B. ischaemum*.

### *Schizachyrium biomass*

The identity of the neighboring plant had a significant effect on *S. scoparium* final total biomass (one-way ANOVA, $df = 3$, $P < 0.002$) (Fig. 2.6). Tukey's a posteriori

multiple comparison tests revealed that *S. scoparium* plants grown with *J. ashei* were significantly smaller than those grown with *B. ischaemum* and those grown in half-sized pots without larvae ($P < 0.05$). *S. scoparium* biomass in pots with *B. ischaemum* and with *P. glandulosa* did not differ statistically from that of *S. scoparium* plants in the half-sized pots ($P > 0.05$). There was also a significant effect of neighbor identity on *S. scoparium* root:shoot mass ratio (one-way ANOVA, df =3, $P < 0.02$). *S. scoparium* plants had significantly lower root:shoot ratios when grown with *J. ashei* than when grown with *B. ischaemum* ($P < 0.05$, Tukey's method) (Fig. 2.7).

## Discussion

Due to the difficulty in quantifying root consumption, I used both the time and the location of larvae on the different pot sides as surrogates for larval feeding on neighboring plants. By all three measures of larval preference, larvae of *Phyllophaga crinita* preferred to eat *Schizachyrium scoparium* roots to the roots of *Juniperus ashei*. There was also a non-significant tendency for these larvae to prefer the roots of *S. scoparium* to those of *Prosopis glandulosa*, but there was no evidence that they differentiated between the roots of *S. scoparium* and *Bothriochloa ishcaemum*, the two grass species. These findings are consistant with others that have found population outbreaks *Phyllophaga* spp. larvae to result in the reduction of perennial grass cover and an increase in the abundance of non-grass species (Ueckert 1979, Coffin et al. 1998).

The preference of *P. crinita* for *S. scoparium* over *J. ashei*, and to a lesser extent over *P. glandulosa*, may be due to differences in the secondary chemistry of these species. *J. ashei* (Adams et al. 1981, Armstrong et al. 1991, Riddle et al. 1996), like other *Juniperus* species (Holcheck et al. 1990, Dearing et al. 2000), can contain high concentrations of phenolic compounds and monoterpenes that are toxic or unpalatable to mammalian browsers (Armstrong et al. 1991, Riddle et al. 1996). As nitrogen-fixing legumes, species of *Prosopis* are known to produce high levels of nitrogen-rich

secondary compounds such as alkaloids (Cates and Rhodes 1977) and phenolic compounds (Janzen 1981, Lyon et al. 1988). In particular, *P. glandulosa* leaves contain high levels of flavanoids (Solbrig et al. 1977). Unfortunately, our understanding of plant defense chemicals in roots and their role in plant-herbivore interactions belowground is extremely limited (Karban and Baldwin 1997, Bezemer et al. 2003, Van der Putten 2003, Blossey and Hunt-Joshi 2003 and references therein). Therefore, I can only speculate that the plants used in this study had similar chemical defense properties in their roots similar to those reported for their foliage.

It is also possible that the relative woodiness of *J. ashei* and *P. glandulosa* roots, compared to the fibrous roots of *S. scoparium,* may have influenced the relative preference of *P. crinita* larvae for *S. scoparium* over *J. ashei*, and perhaps for *S. scoparium* over *P. glandulosa*. The larvae of another species of *Phyllophaga* is known to girdle the woody roots of red pine seedlings (Fowler and Wilson 1971), but there was no evidence that larvae fed on the coarse roots of either of the woody plant species used in this study. However, it is unlikely that root woodiness alone can explain the observed feeding preference of larvae because there were abundant fine roots of *J. ashei* and *P. glandulosa* available throughout the experiment. *P. glandulosa* is a nitrogen-fixing legume, and nodules were observed on the roots of experimental plants. Therefore the roots of *P. glandulosa* may have had relatively high nitrogen content, which to some extent could have counteracted the negative effects of root woodiness and secondary compounds on larval preference.

*Schizachyrium scoparium – performance and implications*

*S. scoparium* plants with *J. ashei* neighbors were significantly smaller than *S. scoparium* plants with *B. ischaemum* neighbors and 'control' *S. scoparium* (grown in half-sized pots without larvae). *S. scoparium* plants grown with *P. glandulosa* were intermediate in size. I propose that these results imply two potentially important consequences for the effect of root herbivory on grassland and savanna communities.

First, the impact of larvae on the growth of this dominant native grass depends on the palatability of neighboring plants. When situated near less palatable plants, *S. scoparium* plants may experience more intense root herbivory that can result in reduced performance (i.e., growth rate, reproductive output, survival) and diminished competitive ability, which in turn can negatively affect the prominence of this dominant grass. Indeed, the reduction of *S. scoparium* abundance in Texas grasslands has been attributed to the selective grazing by cattle (Brown and Stuth 1993, Anderson and Briske 1995), yet little is known about the role that *Phyllophaga crinita*, and possibly other species of white grubs, play in grassland and savanna community composition.

Second, the selective feeding by *Phyllophaga crinita* may facilitate the encroachment of *J. ashei* and *P. glandulosa* into grasslands and savannas. The establishment of woody plants in these systems is often limited by the greater competitive ability of grasses to dominate water in the upper soil layers (Walter 1971, Knoop and Walker 1985, Van Auken and Bush 1997, Van Auken 2000, Jurena and Archer 2003), and many studies demonstrate the competitive suppression of *P. glandulosa* seedlings by grass species in greenhouse (Van Auken and Bush, 1987, 1988, 1989, 1990 and 1997, Bush and Van Auken 1989) and field studies (Bush and Van Auken 1990, 1995). Similar competitive effects of grasses are also reported for other woody seedlings in semi-arid and arid grasslands (Eissenstat and Caldwell 1988, Van Auken and Bush 1990, McPherson 1993). To my knowledge, there are no studies that explicitly examine competition between grasses and *J. ashei*, but studies of *J. pinchotti* and *J. virginiana* in Texas grasslands imply that competition with grasses can limit seedling establishment of these species (McPherson and Wright 1990, Schmidt and Stubbendieck 1993).

While we know little about how herbivores underground affect grass-woody plant interactions, there is considerable evidence that the selective removal of grass foliage by large grazers can facilitate the competitive release of woody seedlings (Madany and West 1983, Milchunas and Lauenroth 1993, McPherson 1993, Archer 1994, Van Auken 2000) by the concomitant reduction of grass root mass (Schuster 1964, Richards 1984, Chiaeb et al. 1996, Dawson et al. 2003, Pucheta et al. 2004). In this study, the preferential

consumption of *S. scoparium* over *J. ashei* and, to a lesser degree, over *P. glandulosa* by *P. crinita* larvae resulted in the direct loss of roots and reduced the total biomass of this dominant grass. This implies that selective feeding by these root herbivores may create 'wet islands', soil patches with increased water availability associated with diminished uptake by damaged grasses (Clements 1984, Brown and Gange 1990). Such changes in soil resource heterogeneity, even at small scales can alter the competitive relationship between plants (Casper and Jackson 1997) and can potentially facilitate the recruitment of woody species (Schlesinger et al. 1990, Jeltsch et al. 1996).

*S. scoparium* plants grown in pots with *B. ischaemum* were similar in size to 'control' *S. scoparium* plants (Fig. 2.6), indicating that *S. scoparium* can compensate for low intensity root herbivory. The different ability of plants to tolerate grazing is known to be an important factor in species replacement in grasslands (Briske and Richards 1994, Anderson and Briske 1995, Olff and Ritchie 1998, Fowler 2002), but we know little about the ability of plants to tolerate, or avoid, root herbivory (Van der Putten 2003). There is evidence that *B. ischaemum*, an invasive exotic grass, can out-compete the native dominant *S. scoparium* (Fowler and Gabbard, *in prep.*). Even though *Phyllophaga crinita* feeding activities did not distinguish between these two grasses, the relative ability of *S. scoparium* and *B. ischaemum* to tolerate root damage may differ, and thus alter the competitive relationship between these co-occurring species.

In conclusion, this study demonstrates the presence of selective root herbivory by *Phyllophaga crinita* among four co-occurring plant species in Texas grasslands and savannas. The effect of these insects on grassland and savanna community structure may be complex based on the palatability and the competitive ability of neighboring plant species (Pacala and Crawley 1992). Future work on how plants avoid or tolerate root loss and how root herbivores modify plant competitive interactions is needed to better understand the role of herbivory in grasslands and savannas, which is currently based almost solely on aboveground interactions.

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Figure 2.1. Photo of experimental pot. Individual plants were grown in half-sized pots (30 cm wide x 30 cm high x 1.5 cm thick) which were combined at the beginning of the feeding trial to form a single large pot (60 cm wide x 30 cm high x 1.5 cm thick).

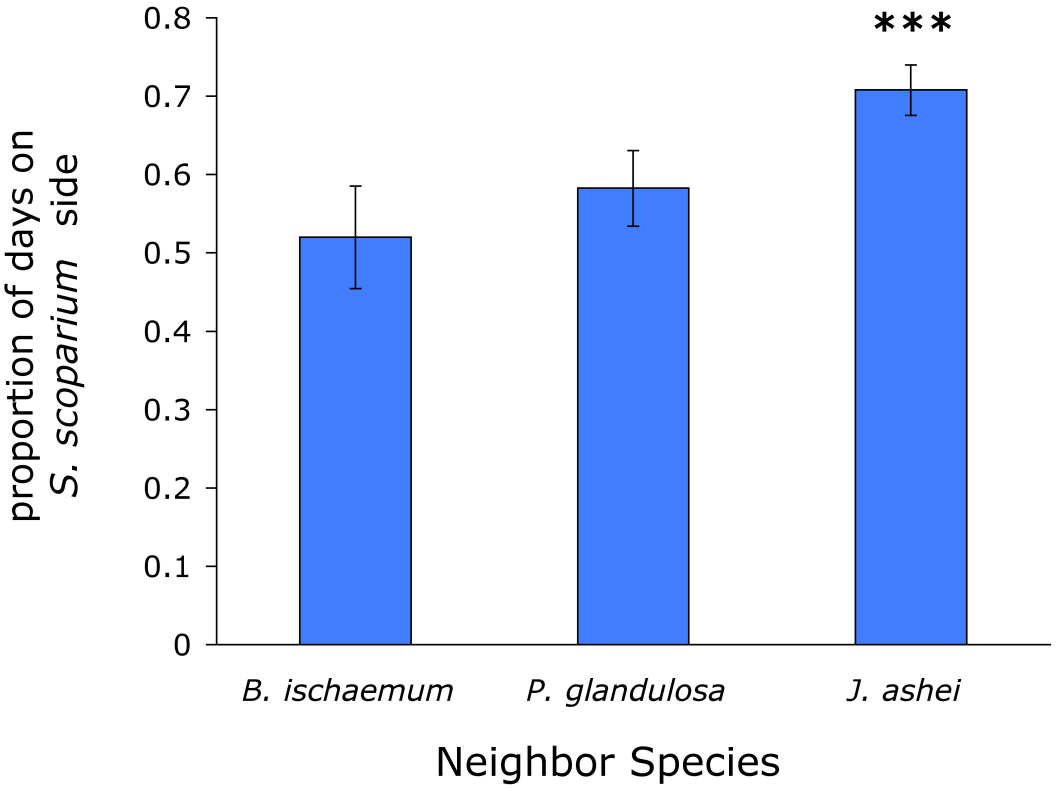


Figure 2.2. Proportion of total active days (mean ± 1 SE) that *P. crinita* larvae were on the *Schizachyrium scoparium* side of pots when paired with *Bothriochloa ischaemum* (n=21), with *Prosopis glandulosa* (n=19), and with *Juniperus ashei* (n=22). Larvae in pots with *J.* ashei spent significantly more time (one-sample t-test on arcsine-transformed data, $P < 0.0001$) on the *S. scoparium* side of pots than the null expectation of 0.50 (i.e. equal time on both pot sides). The proportion of time that larvae spent on the *S. scoparium* side of pots with *B. ischaemum* and with *P. glandulosa* did not differ significantly from 0.50 ($P = 0.78$ and 0.11, respectively). Column heights are the back-transformed means of arcsine-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of arcsine-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of arcsine-transformed values). Therefore the upper and lower error bars are not symmetrical.

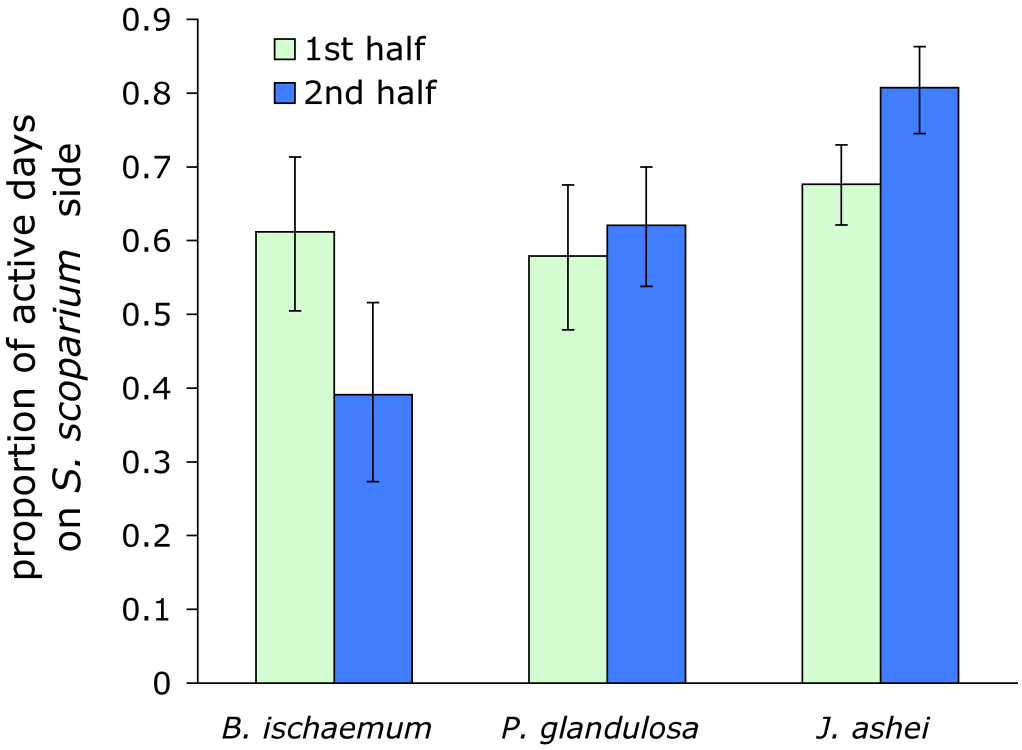


Figure 2.3. Mean (± 1 SE) proportion of days that larvae spent on the *S. scoparium* side of pots in the first and second half of a larva's active feeding period. Differences in first and second half means for all plant combinations are nonsignificant (paired t-test on arcsine-transformed data, all $P > 0.17$). Column heights are the back-transformed means of arcsine-transformed values. Upper error bar = back-transformed ([mean + 1 S.E.] of arcsine-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of arcsine-transformed values). Therefore the upper and lower error bars are not symmetrical.

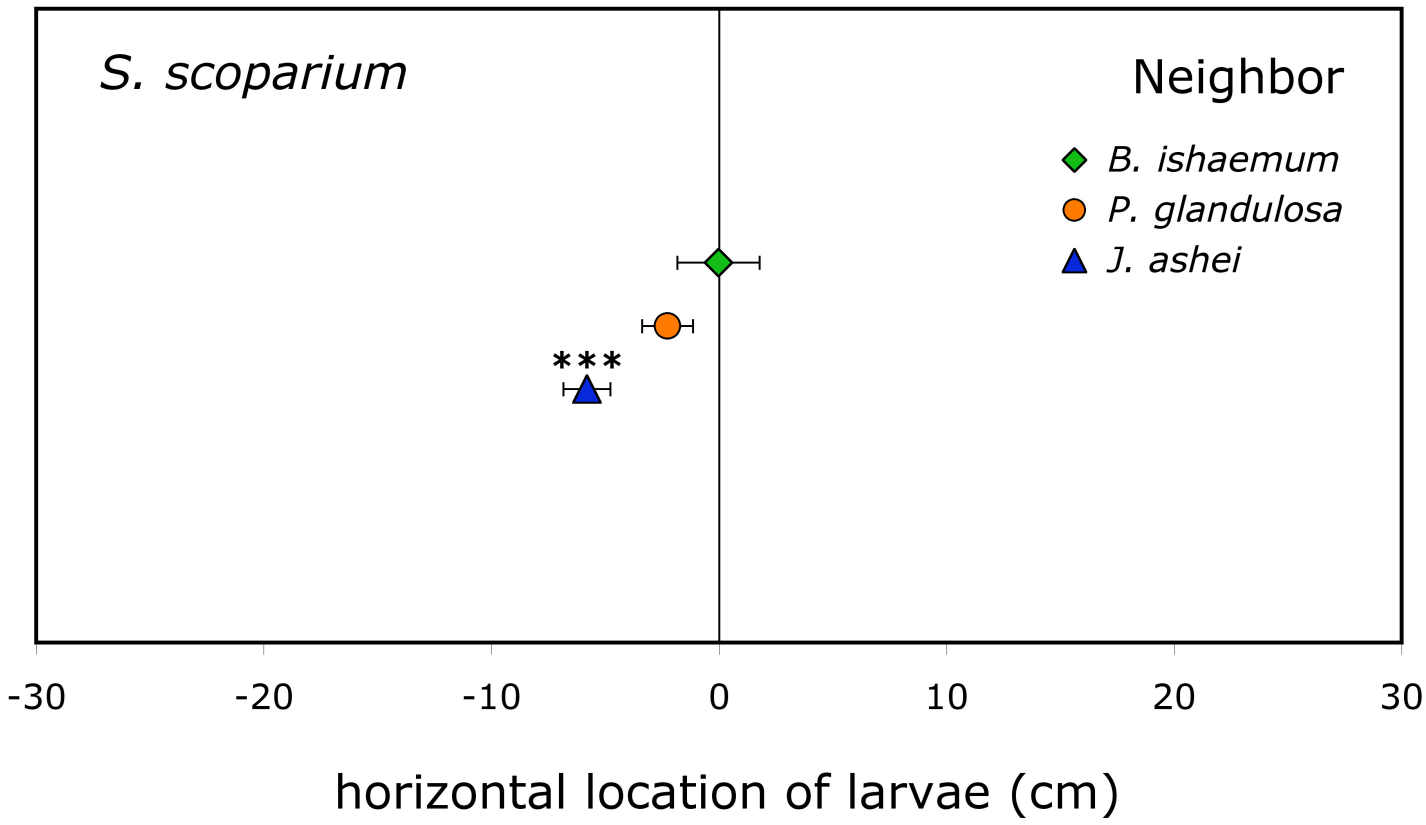


Figure 2.4. Mean horizontal location (± 1 SE) of *Phyllophaga crinita* larvae in pots pairing *Schizachyrium scoparium* with *Bothriochloa ischaemum* (n = 21), with *Prosopis glandulosa* (n = 19), and with *Juniperus ashei* (n = 22). For each plant combination, the mean and standard error were calculated from the mean larval position in each pot. Larval position was significantly associated with the *S. scoparium* side of pots that also had *J. ashei* (one-sample t-test with a null expectation of 0 cm, $P < 0.0001$). There was also a non-significant trend for larvae to be associated with *S. scoparium* in pots with *P. glandulosa* ($P = 0.06$). The x-axis is scaled to represent the actual horizontal distance of pots. The y-axis is unitless.

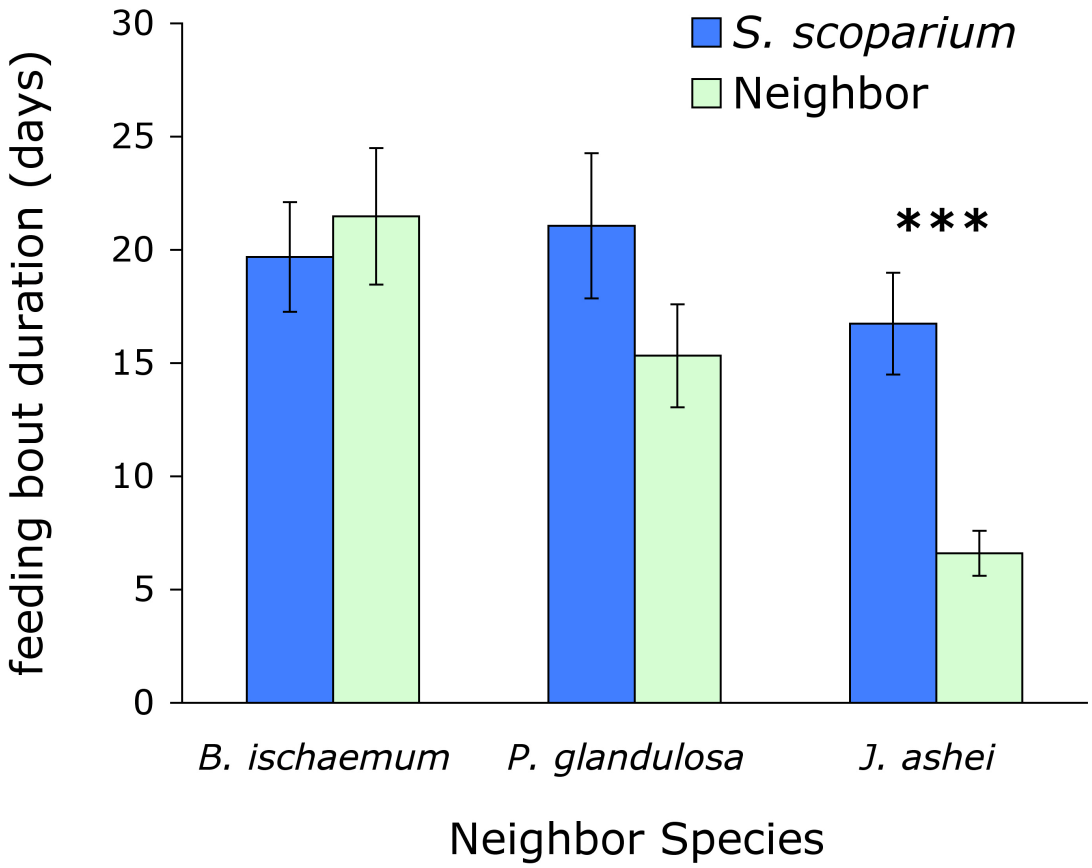


Figure 2.5. Feeding bout duration (mean ± 1 SE) of *Phyllophaga crinita* larvae on *Schizachyrium scoparium* and on neighbor plants in each of the three plant pairings. Feeding bout duration is defined as the number of consecutive days that a larva fed on one pot side until switching to the other pot side. For each plant combination, means are calculated from the mean feeding bout duration in each pot. Feeding bouts were significantly longer on *S. scoparium* than on *J. ashei* (paired t-test, $P < 0.0001$), but feeding bouts did not differ between plant species in the other two pairing treatments ($P > 0.20$ for both). See Figure 1 for sample sizes.

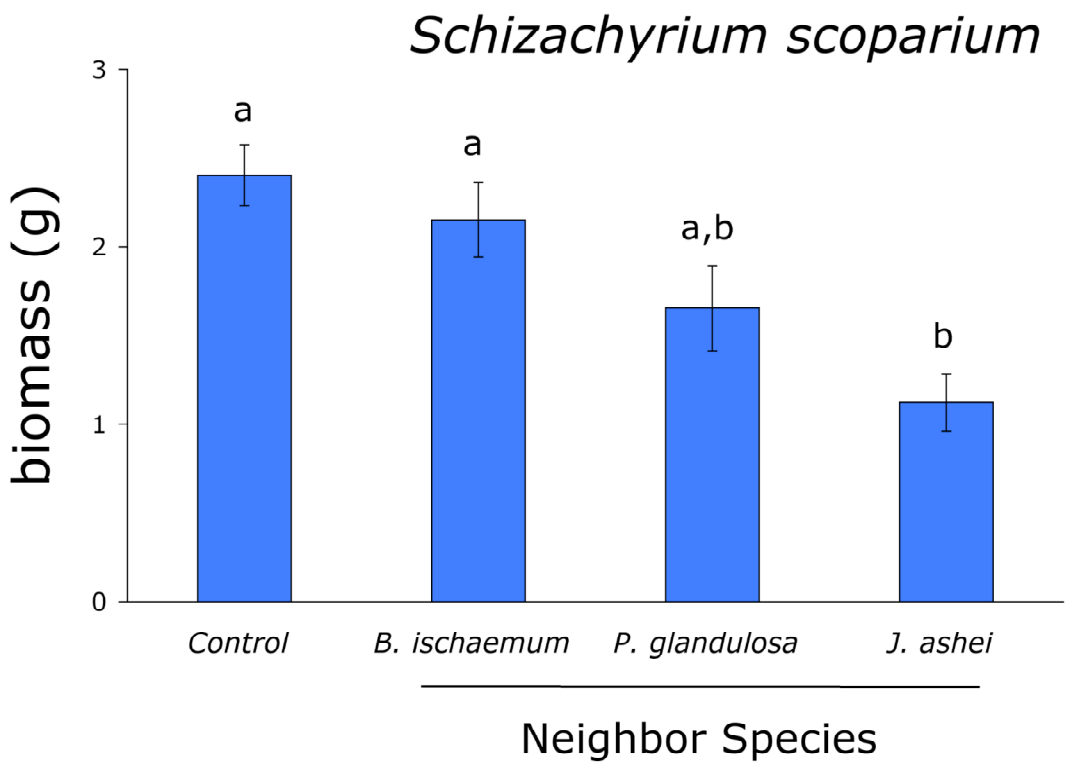


Figure 2.6. Total biomass (mean ± 1 SE) of *Schizachyrium scoparium* when neighbored with *Bothriochloa ischaemum* (n=21), with *Prosopis glandulosa* (n=22), with *Juniperus ashei* (n=22), and in 'control' half-sized pots without larvae (n=6). $P < 0.002$, ANOVA with independent contrasts followed by Tukey's method. Bars that do not share letters have means that are significantly different.

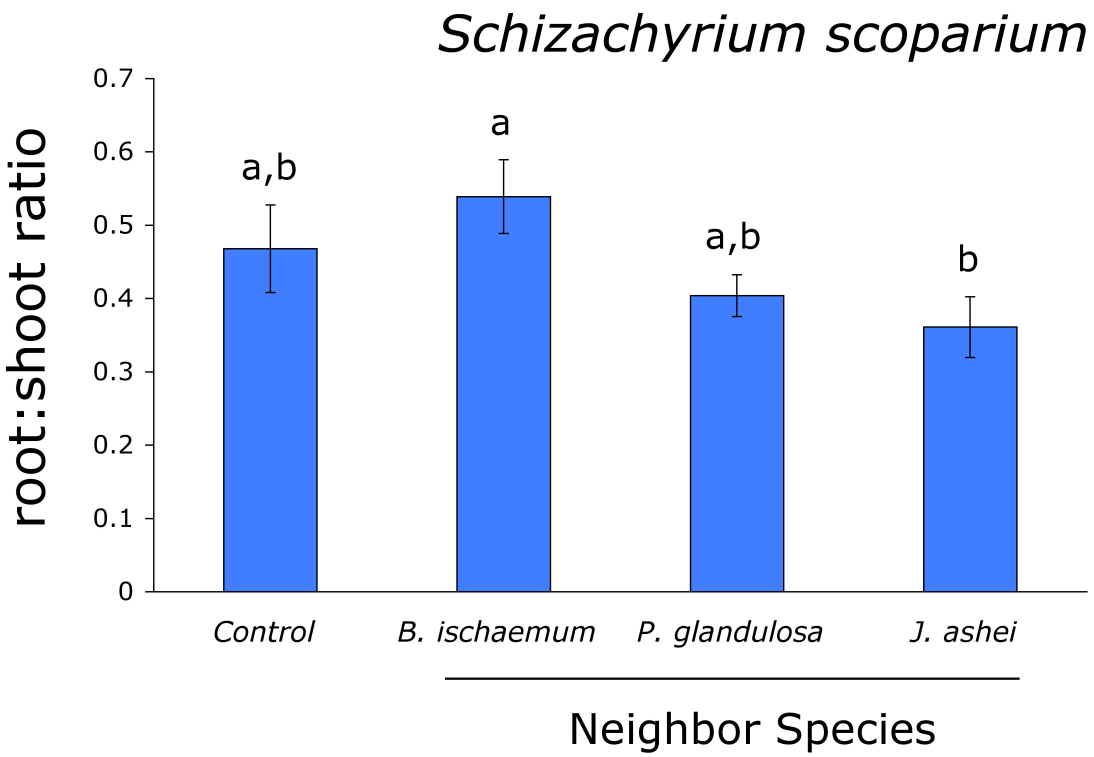


Figure 2.7. Ratio of root to shoot mass (mean ± 1 SE) of *Schizachryium scoparium* neighbored with *Bothriochloa ischaemum* (n=21), with *Prosopis glandulosa* (n=22), with *Juniperus ashei* (n=22), and in 'control' half-sized pots without larvae (n=6). $P < 0.02$, ANOVA with independent contrasts followed by Tukey's method. Bars that do not share letters have means that are significantly different.

# Chapter 3: The effects of root herbivory by *Phyllophaga spp.* (Coleoptera: Scarabaeidae) on grass-woody seedling competition.

## Introduction

Herbivores are important drivers of plant processes across many ecological scales from the individual plant (e.g., physiological responses) to landscape vegetation patterns and ecosystem processes (Harper 1977, Crawley 1983, Huntley 1991, Turner et al. 2001). Herbivory is particularly important in the community structure and dynamics of grasslands and savannas (Dyer et al. 1982, McNaughton 1983, Detling 1988, Archer 1994, Van Auken 2000). Most studies in these systems have focused on the effects of vertebrate grazing, whereas belowground herbivory has received relatively little attention (Crawley 1983, Andersen 1987, Brown and Gange 1990, Huntley 1991, Hunter 2001), even though the effects of belowground herbivory can be quite different from those of aboveground herbivory (Brown and Gange 1989a). However, most of the net primary production and plant biomass is underground in many grasslands and savannas (Coleman 1976, Sims and Singh 1978, Stanton 1988, Jackson et al. 1996), soil resources are often limiting in these systems (Fowler 1986), and the consumption of plants by subterranean invertebrates can be greater than that of aboveground mammals (Smolik et al. 1976, Scott et al. 1979, Stanton et al. 1981, Ingham and Detling 1984). Studies have shown that root herbivory from insects can affect individual plant physiological responses (Gange and Brown 1989, Steinger and Müller-Schärer 1992), reproduction (Maron 1998, Sheppard et al. 1995), and mortality (Ueckert 1979, Gange et al. 1991, Strong et al. 1995). Root herbivores can also affect plant community attributes, such as species composition, species richness and diversity (Brown and Gange 1989b, Coffin et al. 1998, De Deyn et al. 2003), and rates of succession (Brown and Gange 1992, Schädler et al. 2004, De Deyn et al. 2003)

We know particularly little about how insect root herbivores alter belowground competitive interactions among plants in natural systems (Andersen 1987, Brown and Gange 1990, Louda et al. 1990, Hunter 2001). Insect root herbivores may directly alter root system attributes, such as root system size, architecture, and root density, and in doing so can diminish a plant's ability to preempt soil resources from their neighbors (Jackson and Caldwell 1989, Casper and Jackson 1997, Schenk et al. 1999). Many of the studies that have examined the joint effects of root herbivory and competition have focused primarily on the biological control of exotic plant species (Brown and Gange 1990 and Hunter 2001, and references therein; but see Maron 2001 for an example of a native shrub in a coastal dune system). In these studies, insects that feed on a nuisance species have been introduced to reduce its ability to compete with native species, usually grasses (Steinger and Müller-Schärer 1992, McEvoy et al. 1993, Nötzold et al. 1998, Callaway et al. 1999). In this study I investigated the effect of *Phyllophaga spp.* (June beetle) larvae, common native root-feeding insects, on the competitive interaction between a dominant native perennial grass, *Schizachyrium scoparium* (Michx.) Nash (little bluestem grass), and the seedlings of an invasive native woody plant, *Prosopis glandulosa* Torr. (honey mesquite).

Over the last century, *Prosopis glandulosa* has increased in cover and abundance in grasslands and savannas (Archer 1994, Van Auken 2000). The removal of grass foliage, primarily by domestic livestock, can reduce the belowground competitive ability of grasses through the concomitant reduction of grass root mass (Richards 1984, Chiaeb et al. 1996, Dawson et al. 2003, Pucheta et al. 2004), thereby allowing the competitive release of woody seedlings (Madany and West 1983, Adams et al. 1992, Milchunas and Lauenroth 1993, McPherson 1993, Archer 1994, Van Auken 2000, but see Brown and Archer 1999). There are no studies, to my knowledge, that have examined the effect of root consumption by insect herbivores on grass-woody plant interactions in grasslands and savannas.

I examined the separate and joint effects of competition and root herbivory by *Phyllophaga spp.* larvae on *S. scoparium* and *P. glandulosa* performance in two separate

experiments conducted over successive years. In the first year, I examined the effect of high intensity root herbivory (four larvae per pot, which represented a high but realistic density) on *P. glandulosa* seedlings grown in an additive competition experiment with *S. scoparium* (0, 1, and 3 neighboring grass plants in pots). In the second year, I used a range of larval densities (0, 1, and 2 larvae per pot) to determine the effect of low to moderate intensity root herbivory on both *P. glandulosa* seedlings and *S. scoparium* individuals grown alone and together.

*Phyllophaga spp.* (June beetles) larvae, commonly called white grubs, are among the most destructive soil insects in U.S. rangelands (Hewitt et al. 1974) and even their infrequent outbreaks can have long-term consequences for plant community structure (Coffin et al. 1998). These herbivores are thought to feed primarily on the roots of grasses (Hewitt et al. 1974, Potter 1998) and can cause significant reductions in grass cover in grasslands (Schumacher 1959, Ueckert 1979, Coffin et al. 1998). Furthermore, in a separate study I found that *Phyllophaga crinita* Bur., the most common white grub species in Texas (Drees and Jackman 1995, Potter 1998), tended to prefer the roots of *Schizachyrium scoparium* to those of *Prosopis glandulosa* seedlings (see Chapter 2). Therefore, I predicted that the presence of *Phyllophaga spp.* larvae would reduce the competitive effect of *S. scoparium* on *P. glandulosa* seedlings, and thereby potentially facilitate the encroachment of *Prosopis* into grasslands and savannas.

## Methods

### *1998 Experiment*

I grew *Schizachyrium scoparium* and *Prosopis glandulosa* seedlings in a greenhouse at the University of Texas at Austin from seed collected in Travis Co., Texas. I germinated *S. scoparium* seeds in potting soil (Scott's Metro Mix 700™) in early January 1998. Because I wanted *S. scoparium* individuals to be larger than *P. glandulosa*

seedlings, I germinated *P. glandulosa* several months later than *S. scoparium*, in mid-March. *Prosopis glandulosa* seeds were lightly scarified and soaked in water before planting. In early April, I transplanted *P. glandulosa* seedlings and *S. scoparium* individuals, after washing all potting soil from the roots, into separate pots (6 cm diam. x 25 cm deep) containing 1:1 sandy loam and sand. All plants were watered as needed and fertilized monthly (Scott's Peters Professional™ 20-10-20).

I collected larvae of *Phyllophaga spp*. in late July at the University of Texas at Austin's Brackenridge Field Laboratory (BFL), Austin, TX, by excavating a grassy area dominated by *Cynodon dactylon* within 50 m of the experimental garden site. I selected only grubs of *Phyllophaga spp.* of similar size (approx. 2.5-3 cm long). Identification to the species level is difficult without destructive methods (Böving 1942), but it is likely that most, if not all, individuals were *Phyllphaga crinita*. Adults of this species were the most common at trap lights that were checked periodically at the site from April through June. *Phyllophaga fusca and P. congrua* were also trapped at the site.

I transplanted *S. scoparium* and *P. glandulosa* on 4 July into pots in the experimental garden at BFL. I constructed pots (15-cm diam. x 65-cm deep) from PVC pipe that I capped at the bottom with 0.32 mesh hardware cloth. These pots were sunk in the ground leaving approximately 5 cm of the pot above ground level. I filled pots to ground level with a 1:1 sandy loam to sand mixture. *Schizachyrium* individuals 5-9 tillers in size and *Prosopis* individuals 10-13 cm tall (measured from the cotyledon scars) were assigned randomly to pots. To each pot, I added 0.05 L Osmocote™ fertilizer pellets to provide a high level of nutrients and I covered the soil surface in pots with dry grass mulch to reduce evaporation. At the time of transplanting, I also watered plants enough to wet the entire soil column in the pots thoroughly. For approximately three weeks following transplanting, I watered plants (0.5 L of water) every 2-3 days and covered the pots with 63% shade cloth to alleviate transplant shock. On 26 July, I started the watering treatments (described below). On 10 August, I introduced larvae into these pots by placing the larvae in small depressions (~2 cm deep) and covering with soil. Two weeks after the introduction of larvae, many pots were disturbed by animal digging,

presumably by raccoons searching for larvae. To prevent further disturbance, I placed a 2.6 x 5.1 cm wire mesh cage (0.5 m diam. x 0.6 m high) around each pot.

I harvested plants in early December by removing all plant material from pots, including the root systems. I washed soil from the roots using a 1.3 x 1.3 mm wire mesh. All plants were dried for two weeks at 65 C and weighed. I used the cotyledon scar to mark the separation between shoot and root tissues of *P. glandulosa*. I cut all roots of *S. scoparium* at the crown base and separated *S. scoparium* shoot tissue into culm, leaf, and crown tissue. Analyses of the biomass of each of these components of *S. scoparium* shoots were similar to the results of the analyses of combined shoot mass, so only analyses of combined shoot mass are reported here.

*1998 Experimental Design*

The 1998 study had a factorial block design with three levels of competition, two levels of herbivory, two levels of watering, and eight blocks (N=3 x 2 x 2 x 8=96 pots). For the competition treatment I used an additive design: every pot had one target *P. glandulosa* seedling that was either grown alone, or with a low density of *S. scoparium* (one grass plant per pot), or with a high density of *S. scoparium* (three grass plants per pot). In low grass density pots, I positioned *P. glandulosa* and *S. scoparium* individuals on the west and east side of pots, respectively. In high grass density pots, I positioned the three *S. scoparium* individuals equidistant from each other with a single *P. glandulosa* individual in the pot center between the three grasses. To minimize the shading of *P. glandulosa* plants, I tied the leaves of grasses away from *Prosopis* seedlings. There were two levels of the herbivory treatment: each pot received either no larvae or four larvae. Four larvae per pot represents a high, but realistic, larval density at the scale of individual plants (S. Brumbaugh, pers. observ.) and is in agreement with reported outbreak densities (Anonymous 1969). The two levels of watering were 0.25 L (low) and 0.5 L (high) per week. The total volume of water in the low water treatment was similar to the mean monthly precipitation in July and in August (4.85 cm and 5.87 cm, respectively). One

day after each rainfall event in July and August, I gave pots with the high water treatment additional water equaling the previous day's rainfall amount. Even though these amounts were in addition to ambient rainfall, plants still experienced frequent dry soil conditions due to the relatively poor water holding capacity of the soil mixture (1:1 sandy loam and sand) in pots. Also, both July and August were exceptionally hot (0.4-2.3 C above normal monthly high temperatures each month) and dry (1.7-2.9 cm per month below normal monthly precipitation) (recorded at Camp Mabry, Austin, TX; National Weather Service). In contrast to the summer months, September, October, and November had exceptionally high rainfall (4.2-22.7 cm per month above normal monthly precipitation) and watering treatments were abandoned because pots designated to have the low water treatment frequently had saturated soils. During this period and for the remainder of the study, I watered all pots with equal amounts as needed.

*1999 Experiment*

For the 1999 experiment, I repeated all methods for growing *Prosopis glandulosa* and *Schizachyrium scoparium* in the greenhouse and in experimental pots at BFL as described in the 1998 experiment, with the exception that cages were installed at the beginning of the experiment. The collection of *Phyllophaga* larvae was the same as in 1998, as well. Again, adults of *P. crinita* were the most commonly trapped species at the site and their larvae were assumed to be most, or all, of the larvae used in the experiment. Also, the dates of events (month and week) in 1999 were similar (usually within a week) to those in the 1998 experiment.

*1999 Experimental Design*

In the 1999 study, both *P. glandulosa* and *S. scoparium* were grown alone and in combination. Each plant combination received one of three levels of larval density: no larvae, one larva, or two larvae per pot. Each plant combination x larval density

treatment was present in each of seven blocks, for a total of 63 pots (3 plant combinations x 3 larval densities x 7 replicates). *Schizachyrium* individuals and *Prosopis* individuals were similar in size to those used in the 1998 study and were assigned randomly to pots. All methods used for experimental pots in 1998 were repeated in the 1999 experiment with the exception of the plant and larval densities associated with the different treatment levels and the fact that the 1999 experiment had no water treatment; instead, I watered all pots with equal amounts as needed throughout the study to prevent plant mortality. I used the same block and pot locations as were used in the 1998 study.

***Statistical Analyses***

I performed all statistical analyses with SAS v8.0 (SAS Institute 1999). Root:shoot mass ratio was calculated as the total root mass divided by the total shoot mass for each plant separately.

*1998 Prosopis glandulosa – biomass and root:shoot ratio*

*P. glandulosa* 1998 total biomass, root biomass, shoot biomass, and root:shoot ratio were each log-transformed before analysis to improve normality of residuals and homogeneity of variances. The effect of both block and water were nonsignificant in 1998 (all $P>0.88$ and $P>0.18$, respectively; Kruskal-Wallis nonparametric test) and therefore I dropped these factors from these analyses. In 1998, the combination of deaths of *P. glandulosa* in pots with grubs and losses of pots to animal disturbance resulted in an unbalanced design, with one treatment combination completely missing (*P. glandulosa* alone in pots with grubs). Therefore I analyzed *P. glandulosa* biomass with planned contrasts that tested

(1) the difference, in pots without grubs, between *P. glandulosa* biomass when grown alone and when grown with one *S. scoparium* plant,

(2) the difference between *P. glandulosa* biomass when grown with one and with three *S. scoparium* plants (pooling grub treatments and omitting pots without *S. scoparium*),

(3) the difference, in pots with *S. scoparium* plants, between *P. glandulosa* biomass when grown with and without grubs (pooling pots with one and three *S. scoparium* plants) and omitting pots without *S. scoparium*).

(4) the interaction effect on *P. glandulosa* biomass between grub presence and the number of *S. scoparium* plants in the pots, omitting pots without *S. scoparium*.

Contrasts (2), (3), and (4) together are similar to a two-way ANOVA on a dataset from which pots without *S. scoparium* have been deleted. Note that the total number of contrasts (4) is no more than the model degrees of freedom (model df = 4, because only 5 of the 6 planned treatment combinations had surviving *P. glandulosa* plants). SAS PROC GLM was used to do these analyses.

*1998 Schizachyrium scoparium – biomass*

Only total biomass of *S. scoparium* in 1998 was analyzed. Total biomass was analyzed with a two-way ANOVA in which *S. scoparium* density (one or three plants) and larval presence or absence were the main effects. These data were not transformed for analysis. Because the effect of both block and water were nonsignificant in 1998 ($P = 0.49$ and $P = 0.62$, respectively; Kruskal-Wallis nonparametric test), I dropped these factors from the analysis.

*1998 Prosopis glandulosa – survival*

It was not possible to analyze the effects of competition and herbivory on survival simultaneously, because there were no deaths of *P. glandulosa* in pots without larvae and few *P. glandulosa* survivors in pots with larvae but without competitors. Therefore, I constructed separate two-way contingency tables and used chi-square analysis to test the

effect of larvae and the effect of grass density on *Prosopis* survival status (alive/dead). Chi-square analyses were done with SAS PROC FREQ.

1998 *S. scoparium* survival

There were only five *S. scoparium* deaths in 1998, too few to analyze survival.

*1999 Prosopis glandulosa – biomass and root:shoot ratio*

*P. glandulosa* 1999 total biomass, root biomass, shoot biomass, and root:shoot ratio were each log-transformed before analysis to improve normality of residuals and homogeneity of variances. I analyzed *P. glandulosa* 1999 total biomass, root biomass, shoot biomass, and root:shoot ratio separately with three-way ANOVAs in which *S. scoparium* presence/absence, grub density (0, 1, or 2 per pot) and block were all treated as fixed main effects.

*1999 Schizachyrium scoparium – biomass and root:shoot ratio*

*S. scoparium* 1999 total biomass, root biomass, shoot biomass, and root:shoot ratio were each log-transformed before analysis to improve normality of residuals and homogeneity of variances. *S. scoparium* total, shoot, and root biomass, and root:shoot ratio biomass in 1999 were each analyzed with a three-way ANOVA in which *P. glandulosa* presence/absence, grub density (0,1, or 2 per pot), and block were all treated as fixed main effects.

*1999 Prosopis glandulosa – survival*

There were only three deaths of *P. glandulosa* in 1999, too few to analyze.

*1999 Schizachyrium scoparium – survival*

There were no *S. scoparium* deaths in 1999.

## Results

*1998 Prosopis glandulosa – survival*

*Prosopis glandulosa* seedling survival rates were significantly lower in pots with four larvae than in pots with no larvae (chi-square test, $\chi^2 = 57.8$, df = 1, $P < 0.0001$) (Fig. 1).

*1998 Prosopis glandulosa – growth*

On average, the largest *Prosopis glandulosa* seedlings were in the pots without larvae or grass plants (Fig. 2). The presence of even one grass plant in the pot significantly reduced *P. glandulosa* size (Table 3.1): in pots without larvae, the average total, shoot, and root biomass of *P. glandulosa* seedlings grown alone were about four times as large as those of seedlings grown with one grass plant (Figures 3.2 and 3.3). Three grass plants had a greater negative effect than one grass plant: averaged over larval treatments, *P. glandulosa* seedlings in pots with three grass plants were significantly smaller than seedlings in pots with one grass plant. The presence of larvae was also associated with significantly smaller *P. glandulosa* seedlings. Comparing only pots with grass plants (to avoid confounding the effects of larvae with those of grass plants), seedlings were on average approximately 70% smaller in pots with larvae than in pots without larvae. There was no evidence that the effects of larvae and of grass plants interacted in their effects on *P. glandulosa* size.

The only significant contrast of root:shoot ratios was between plants grown alone (no larvae, no grass plants) and plants grown with one grass plant and no larvae (Table 3.1); *P. glandulosa* seedlings grown alone had significantly lower root:shoot ratios than did seedlings grown with one grass plant (Fig 3.4). Although the differences between each pair of treatment combinations was not tested, note that the root:shoot ratio of seedlings grown alone was lower than that of seedlings in any other treatment combination. In the presence of one or more grass plants, there was a tendency for seedlings in pots with larvae to have, on average, lower root:shoot ratios than seedlings in pots without larvae ($P$=0.0500; Table 3.1).

*1998 Schizachyrium scoparium – growth*

There was a non-significant trend for greater combined biomass of *Schizachyrium scoparium* in pots with three grass plants than with one grass plant (Table 3.2, Fig. 3.5). Averaged over the two grass densities, the presence of larvae resulted in a significant reduction of *Schizachyrium* biomass (Table 3.2, Fig 3.5).

*1999 Prosopis glandulosa – growth*

The presence of grass plants in a pot significantly reduced the size of *P. glandulosa* seedlings by two-thirds (Table 3.3, Fig. 3.6). There was no evidence for any effect of the presence and density of larvae on the total, shoot, and root mass of *P. glandulosa* seedlings (Figs. 3.6, 3.7 & 3.8), nor was there any evidence for a significant interaction between the effects of grass plants and larvae. There were no detectable effects of the treatments upon root:shoot ratio.

*1999 Schizachyrium scoparium – growth*

*Schizachyrium scoparium* plants were much larger than *Prosopis glandulosa* seedlings (compare the axes of Figs. 3.6 and 3.9). The presence of larvae, significantly reduced total biomass and root mass of *S. scoparium*, on average, approximately 22% and 30%, respectively, but did not affect root:shoot ratio (Table 3.4, Figs. 3.9, 3.10 and 3.11). However, there was no significant difference between the effects of one larva and two larvae on *S. scoparium* mass (Tukey's multiple comparison tests, $P > 0.05$). The presence of *P. glandulosa* was associated with greater *S. scoparium* root mass, but only in pots with no larvae (significant interaction effect, Table 3.4). There was a significant direct effect of *P. glandulosa* on *S. scoparium* root:shoot ratio, which was approximately 36% higher in the presence of *P. glandulosa*.

## Discussion

*Joint effects of competition and root herbivory*

In general, there was no significant interaction between the effects of competition and root herbivory on the size of *Prosopis glandulosa* or *Schizachyrium scoparium*, except for a marginally significant effect on *S. scoparium* root mass in 1999. Because statistical analyses of plant biomass were performed with log-transformed values (except for total *S. scoparium* biomass in pots in 1998), the factors in the model are multiplicative in their effect, rather than additive. Therefore, in the absence of a significant interaction effect, the joint effect of competition and root herbivory on plant size was simply the product of the relative effects of each of these factors (Fowler and Rausher 1985). Therefore, competitor presence and root herbivory each had a greater absolute effect on target plant size when the other factor was absent. In other words, plants grown without competitors were larger, and therefore experienced a greater absolute reduction in

biomass from root herbivory than did plants grown with competitors. Likewise, plants grown without herbivores were larger and therefore experienced a greater absolute reduction in biomass from competition than plants grown with herbivores. These results are consistent with those of the meta-analysis by Gurevitch et al. (2000) that found the effects of competitors to be greater in the absence of predators, and vice versa.

*Direct effects of competition*

*Schizachyrium scoparium* had a strong competitive effect on *Prosopis glandulosa* seedlings. The presence of one grass plant in pots resulted in a similar reduction in *Prosopis* size (~70%) in both years. Pots with three grass plants had about 20% more grass biomass than pots with one grass plant, although this was not a significant difference ($P = 0.09$). Overall, these results are similar to those of other greenhouse (Van Auken and Bush, 1987, 1988, 1989, 1990 and 1997, Bush and Van Auken 1989) and field studies (Bush and Van Auken 1990, 1995), which have also found a competitive suppression of *Prosopis glandulosa* seedlings by grass species. There was no indication that *Prosopis glandulosa* presence affected the size of *S. scoparium* individuals in 1999. This was not surprising because *P. glandulosa* individuals in pots with grass plants were considerably smaller (about one tenth the size) than *S. scoparium* individuals and a plant's competitive effect is often proportional to its size (Miller and Werner 1987, Goldberg 1990).

*Direct effects of root herbivory*

The high larval density (four larvae per pot) in 1998 significantly reduced *P. glandulosa* seedling survival. The high density of root herbivores in 1998 also had a strong negative effect on *P. glandulosa* growth and on the total grass biomass in pots (Fig. 3.12). Population outbreaks of white grubs are known to cause extensive damage to many managed grass systems, including crops (Teetes 1973), pastures (Graber et al.

1931), and turfgrasses (Potter 1998). In northern forests of the United States, *Phyllphaga spp*. larvae are also an important cause of red pine seedling mortality (Fowler and Wilson 1971). The few accounts of *Phyllophaga spp.* larval outbreaks in natural grasslands and rangelands report significant impacts on plant mortality and cover (Schumacher 1959, Ueckert 1979). As Coffin et al. (1998) note, even infrequent episodes of intense root herbivory by *Phyllophaga spp.* larvae could have profound long-term effects on successional patterns and community dynamics.

The low densities of larvae in 1999 had no discernible effect on *Prosopis* growth, although visible inspection of the roots did show signs of root consumption. The extent to which plants can replace tissues consumed by herbivores (i.e. compensatory growth) has received considerable debate (see Belsky 1986, McNaughton 1986). There is evidence that many, if not most, plants can compensate for root loss (Andersen 1987, Brown and Gange 1990, Hunter 2001), but the degree to which they can do so will depend, in part, on the amount of carbohydrate reserves that can be translocated for new growth. In a study of the feeding behavior of *Phyllophaga crinita* larvae (the most common species of *Phyllophaga* at the study site, based on adult captures), I observed larvae feeding only on the fine roots of *Prosopis* seedlings (see Chapter 2), thus preserving the majority of the root mass (which is in the woody tap root) that likely serves as an important source of non-structural carbohydrates for fine root replacement. Of the seedlings that died in 1998, the entire root system was removed near the soil surface. These findings suggest that the timing of larval outbreaks relative to seedling size may also be an important determinant of seedling performance; larger seedlings will have woodier tap roots that are more apt to resist damage (Crawley 1983). Further experiments examining the effects of density and seedling size are needed to better understand this interaction.

In contrast, the presence of larvae caused a moderate, but significant, reduction in *Schizachrium* root biomass and total biomass (Table 3.4). The 'damage-threshold' of grasses, defined as the amount of root damage before there is a noticeable reduction in foliage, can be as high as 50-60% (Davidson 1979). Other studies involving the root

feeding of *Phyllophaga spp.* larvae on *Muhlenbergia quadridentata* (Morón-Ríos et al. 1997) and of *Sericesthis nigrolineata* larvae (Coleoptera: Scarabaeidae) on *Lolium perenne* in pastures (Ridsdill Smith 1977) also reported no significant reduction in foliage yield associated with moderate intensity root herbivory. This implies that the effect of belowground herbivory in grasslands may often go unnoticed by the simple observation of aboveground plant response.

The root systems of *Prosopis* seedlings and *Schizachyrium* likely differ in nutritional quality and secondary metabolite concentrations in ways that influence larval feeding behavior. Leguminous nitrogen-fixers, such as *P. glandulosa*, have high nitrogen content in tissues as well as high levels of nitrogen-rich secondary compounds (e.g. alkaloids and phenolics) (Cates and Rhodes 1977). Although plant tissue was not analyzed, most *Prosopis* seedlings in this study had root nodules, and therefore were presumably fixing nitrogen. In contrast, grasses are generally thought to have high C:N ratios but to lack significant quantities of chemical defenses (McNaughton 1983, Moles and Joern 1993). In a previous study, there was a tendency for *Phyllophaga crinita* larvae to prefer the roots of *S. scoparium* to those of *P. glandulosa* (see chapter 2). In this study, however, it appeared that both species were being eaten; *Prosopis* was not completely protected by secondary compounds and *Schizachyrium* was not completely protected by a high C:N ratio. In general, plant nutritional properties and defense strategies below ground are poorly understood. This remains an important area of future work in understanding plant-herbivore interactions (Andersen 1987, Brown and Gange 1990, Karban and Baldwin 1995).

*Importance of root herbivory on plant interactions*

There was little evidence that root herbivory altered the effect of competition (and vice versa) between *Schizachyrium scoparium* and *Prosopis glandulosa*. Therefore, these findings did not support my initial hypothesis that white grubs may facilitate *P. glandulosa* recruitment by decreasing the competitive domininance of *S. scoparium*. It

appears, instead, that outbreaks of white grubs may further limit *Prosopis* recruitment through direct mortality and reduced growth. At high larval density, *P. glandulosa* seedlings in pots with grasses, on average, were ~70% smaller (Fig. 3.2). Likewise, the total biomass of *S. scoparium* plants in pots (i.e., the summed biomass of all plants in each pot), averaged across the grass density treatments, was reduced by almost 80% (Fig 3.5). These dramatic reductions in plant biomass indicate that episodes of high white grub density can be significant forms of disturbance in grasslands and savannas (Ueckert 1979, Coffin et al. 1998).

Under conditions of lower white grub densities (1-2 larvae per pot), *S. scoparium* and *P. glandulosa* individuals exhibited similar relative reductions in size. Specifically, *Schizachyrium* individuals, on average, were about 22% smaller in pots with one and two larvae. Likewise, *P. glandulosa* seedlings were 26% smaller (a non-significant difference), on average, in pots with larvae (32% with one larva and 20% with two larvae). In contrast, competition with *S. scoparium* caused a ~70% reduction in *P. glandulosa* size. These results suggest that in non-outbreak years, competition with grasses will have a greater effect on *P. glandulosa* seedling performance than root herbivory by these insects.

Other studies that have examined the separate and joint effects of root herbivory and competition have focused primarily on the use of biocontrol agents to decrease the competitive ability of nuisance plant species (McEvoy et al. 1993). In these studies, the effect of root herbivory on competitive interactions and the relative importance of these factors have been mixed. For instance, Steinger and Müller-Schärer (1992) found that moderate root herbivory by *Agapeta zoegana* (knapweed root moth) did not alter the competitive ability of its host, *Centaurea maculosa* (knapweed) and it was concluded that competition with the grass, *Festuca pratensis*, had a greater effect on *C. maculosa* performance than did root herbivory. Yet Callaway et al. (1999) found that *A. zoegana* did alter the competitive effect of *C. maculosa* on a native grass (*Festuca idahoensis*), but the direction of this interaction was surprising: damaged *C. maculosa* plants became stronger competitors. In contrast, purple loosestrife (*Lythrum salicaria*) plants targeted

by the insect root herbivore, *Hylobius transversovittatus,* showed a reduced ability to compete with a grass, *Phleum pratense* (Nötzold et al. 1997). In this case, it was determined that root herbivory had a larger effect than grass competition in reducing purple loosestrife performance, but the effects of herbivory were largely delayed until the second year of the study.

A few studies suggest that delayed effects of root herbivory may not be evident in studies that occur over a single growing season (Andersen 1987, Nötzold et al. 1997, Maron 1998), and this possibility cannot be ruled out in this study. The loss of carbohydrate reserves in roots may primarily influence a plant's ability to generate new growth the following growing season, or later (Mooney and Billings 1960). For instance, Maron (1998) found that it took bush lupine (*Lupinus arboreus*) three years to exhibit a reduction in reproduction following root damage. Moreover, soil resource availability (Graber et al. 1931, Radcliffe 1971, Ladd and Buriff 1979, Prestidge et al. 1985) can alter the impact of root herbivores on plant performance, and thereby alter plant interactions (Steinger and Müller-Schärer 1992). In all, these studies suggest that the influence of belowground herbivores on plant communities is likely to be complex and dependent on species-specific traits and abiotic conditions.

*Implications for Prosopis glandulosa establishment*

The modification of plant competitive abilities by herbivores is thought to play important role in the encroachment of woody plants in many grasslands and savannas (Archer 1994, Scholes and Archer 1997, Van Auken 2000, Sankaran et al. 2004). In many of these systems, competition for resources under ground, especially water, is considered key for plant interactions (Fowler 1986, Wilson 1993, Wilson and Tilman 1993, Jeltsch et al. 1996. Scholes and Archer 1997, Van Auken 2000) and many studies show that woody seedling establishment is limited by the superior ability of grasses to take up water in the upper soil layers (Knoop and Walker 1985, Kolb and Robberecht 1996. Van Auken and Bush 1997, Jurena and Archer 2003). There is also ample

evidence that intense selective grazing and the removal of grass foliage can cause a concomitant reduction in grass root mass (Richards 1984, Chiaeb et al. 1996, Dawson et al. 2003, Pucheta et al. 2004) allowing the competitive release of woody seedlings (Madany and West 1983, Adams et al. 1992, Milchunas and Lauenroth 1993, McPherson 1993, Archer 1994). It appears, however, that the *Pyllophaga spp.* in this study consume the roots of both *S. scoparium* and *P. glandulosa* and had similar relative effects on both species. In doing so, these herbivores may further limit *P. glandulosa* establishment during outbreak years, but at lower densities their effect on *P. glandulosa* is subordinate to the strong competitive effects of grasses.

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Table 3.1. Sums of squares (Type III) table for independent contrasts on *Prosopis glandulosa* total biomas, root mass, shoot mass, and root:shoot mass ratio in 1998. For each growth measure, four contrasts were done to test: (1) the effect of competition with one *S. scoparium* plant and with no larvae present, (2) the main effect of competition in pots with *S. scoparium* neighbors, (3) the main effect of herbivory in pots with grass neighbors, and (4) the interaction between the effects of competition and herbivory in pots with grass neighbors. Analyses were done on log-transformed data.

| | LN(Total Biomass) | | | | |
|---|---|---|---|---|---|
| *Factor* | *df* | *SS* | *MS* | *F* -value | *P* -value |
| Model | 4 | 99.45 | 24.86 | 4.07 | <0.0001 |
| In pots with no larvae | | | | | |
| Alone v. w/ 1 grass | 1 | 13.39 | 13.39 | 29.12 | <0.0001 |
| In pots with grass plants | | | | | |
| Competition (C) - w/ 1 grass v. w/ 3 grasses | 1 | 12.25 | 12.25 | 26.65 | <0.0001 |
| Herbivory (H) - no larvae v. 4 larvae | 1 | 15.7 | 15.7 | 34.14 | <0.0001 |
| C x H | 1 | 0.73 | 0.73 | 1.59 | 0.21 |
| Error | 58 | 26.69 | 0.46 | | |

| | LN(Root mass) | | | | |
|---|---|---|---|---|---|
| *Factor* | *df* | *SS* | *MS* | *F* -value | *P* -value |
| Model | 4 | 93.02 | 23.25 | 57.01 | <0.0001 |
| In pots with no larvae | | | | | |
| Alone v. w/ 1 grass | 1 | 11.38 | 11.38 | 27.91 | <0.0001 |
| In pots with grass plants | | | | | |
| Competition (C) - w/ 1 grass v. w/ 3 grasses | 1 | 13.24 | 13.24 | 32.46 | <0.0001 |
| Herbivory (H) - no larvae v. 4 larvae | 1 | 14.69 | 14.69 | 36 | <0.0001 |
| C x H | 1 | 0.15 | 0.15 | 0.37 | 0.55 |
| Error | 57 | 23.25 | 0.41 | | |

Table 3.1 (continued). Sums of squares (Type III) table for independent contrasts on *Prosopis glandulosa* total biomas, root mass, shoot mass, and root:shoot mass ratio in 1998. For each growth measure, four contrasts were done to test: (1) the effect of competition with one *S. scoparium* plant and with no larvae present, (2) the main effect of competition in pots with *S. scoparium* neighbors, (3) the main effect of herbivory in pots with grass neighbors, and (4) the interaction between the effects of competition and herbivory in pots with grass neighbors. Analyses were done on log-transformed data.

| | LN(Shoot mass) | | | | |
|---|---|---|---|---|---|
| *Factor* | *df* | *SS* | *MS* | *F* -value | *P* -value |
| Model | 4 | 103.16 | 25.79 | 48.81 | <0.0001 |
| In pots with no larvae | | | | | |
| Alone v. w/ 1 grass | 1 | 15.8 | 15.8 | 29.91 | <0.0001 |
| In pots with grass plants | | | | | |
| Competition (C) - w/ 1 grass v. w/ 3 grasses | 1 | 13.48 | 13.48 | 25.51 | <0.0001 |
| Herbivory (H) - no larvae v. 4 larvae | 1 | 12.28 | 12.28 | 23.24 | <0.0001 |
| C x H | 1 | 0.83 | 0.83 | 1.58 | 0.21 |
| Error | 58 | 30.65 | 0.53 | | |

| | LN(Root:Shoot mass ratio) | | | | |
|---|---|---|---|---|---|
| *Factor* | *df* | *SS* | *MS* | *F* -value | *P* -value |
| Model | 4 | 1.09 | 0.27 | 4.35 | 0.004 |
| In pots with no larvae | | | | | |
| Alone v. w/ 1 grass | 1 | 0.36 | 0.36 | 5.77 | 0.02 |
| In pots with grass plants | | | | | |
| Competition (C) - w/ 1 grass v. w/ 3 grasses | 1 | 0.0002 | 0.0002 | 0 | 0.95 |
| Herbivory (H) - no larvae v. 4 larvae | 1 | 0.25 | 0.25 | 4.01 | 0.05 |
| C x H | 1 | 0.19 | 0.19 | 2.96 | 0.09 |
| Error | 57 | 3.57 | 0.06 | | |

Table 3.2. Two-way ANOVA results for total *Schizachyrium scoparium* biomass in pots (all *S. scoparium* plants in each pot combined) in 1998. The main effects of grass density (1 grass and 3 grasses) and herbivory (0 and 4 larvae) are both treated as fixed effects. Type III sums of squares are reported.

| | Total biomass | | | | |
|---|---|---|---|---|---|
| *Source of Variation* | *df* | *SS* | *MS* | *F* -value | *P* -value |
| Density (1 grass v. 3 grasses) | 1 | 464.08 | 464.08 | 2.90 | 0.09 |
| Herbivory (no larvae v. 4 larvae) | 1 | 19966.25 | 19966.25 | 124.89 | <0.0001 |
| Density x Herbivory | 1 | 118.50 | 118.50 | 0.74 | 0.39 |
| Error | 52 | 8313.34 | 159.87 | | |

Table 3.3. Three-way ANOVA results for *Prosopis glandulosa* total biomass, root mass, shoot mass, and root:shoot mass ratio in 1999. The main effects of block, competition (0 and 1 *S. scoparium* neighbor), and herbivory (0, 1, and 2 larvae) were all treated as fixed effects. Analysis for all four growth measures were done on log-transformed data. Type I sums of squares are reported.

| | Total biomass | | | | Root mass | | | | Shoot mass | | | | Root:Shoot mass ratio | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of Variation* | *df* | *SS* | *F-value* | *P-value* | *df* | *SS* | *F-value* | *P-value* | *df* | *SS* | *F-value* | *P-value* | *df* | *SS* | *F-value* | *P-value* |
| Block | 6 | 7.45 | 1.40 | 0.25 | 6 | 6.46 | 1.17 | 0.35 | 6 | 8.14 | 1.32 | 0.28 | 6 | 1.96 | 1.96 | 0.11 |
| Competition (C) | 1 | 12.61 | 14.26 | <0.001 | 1 | 12.51 | 13.58 | 0.001 | 1 | 14.50 | 14.10 | <0.001 | 1 | 0.07 | 0.44 | 0.51 |
| Herbivore density (H) | 2 | 0.50 | 0.28 | 0.76 | 2 | 0.62 | 0.34 | 0.72 | 2 | 0.44 | 0.21 | 0.81 | 2 | 0.07 | 0.21 | 0.81 |
| C x H | 2 | 1.33 | 0.75 | 0.48 | 2 | 1.71 | 0.93 | 0.41 | 2 | 0.44 | 0.21 | 0.81 | 2 | 0.42 | 1.25 | 0.30 |
| Error | 27 | 23.87 | | | 27 | 24.89 | | | 27 | 27.76 | | | 27 | 4.50 | | |

Table 3.4. Three-way ANOVA results for *Schizachyrium scoparium* total biomass, root mass, shoot mass, and root:shoot mass ratio in 1999. The effects of block, competition (0 and 1 *P. glandulosa* neighbor), and herbivory (0, 1, and 2 larvae) were all treated as fixed effects. Analyses for all four growth measures were done on log-transformed data. Type I sums of squares are reported.

| | Total mass | | | | Root mass | | | | Shoot mass | | | | Root:Shoot mass ratio | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Source of Variation* | *df* | *SS* | *F-value* | *P-value* | *df* | *SS* | *F-value* | *P-value* | *df* | *SS* | *F-value* | *P-value* | *df* | *SS* | *F-value* | *P-value* |
| Block | 6 | 0.85 | 1.98 | 0.10 | 6 | 0.47 | 1.24 | 0.31 | 6 | 1.43 | 1.50 | 0.21 | 6 | 0.58 | 0.43 | 0.85 |
| Competition (C) | 1 | 0.02 | 0.31 | 0.58 | 1 | 0.21 | 3.39 | 0.08 | 1 | 0.30 | 1.89 | 0.18 | 1 | 1.02 | 4.51 | 0.04 |
| Herbivore density (H) | 2 | 0.59 | 4.11 | 0.03 | 2 | 1.25 | 9.95 | <0.001 | 2 | 0.39 | 1.22 | 0.31 | 2 | 0.49 | 1.08 | 0.35 |
| C x H | 2 | 0.22 | 1.56 | 0.23 | 2 | 0.61 | 4.82 | 0.02 | 2 | 0.09 | 0.28 | 0.76 | 2 | 0.28 | 0.62 | 0.54 |
| Error | 30 | 2.14 | | | 30 | 1.89 | | | 30 | 4.78 | | | 30 | 6.79 | | |

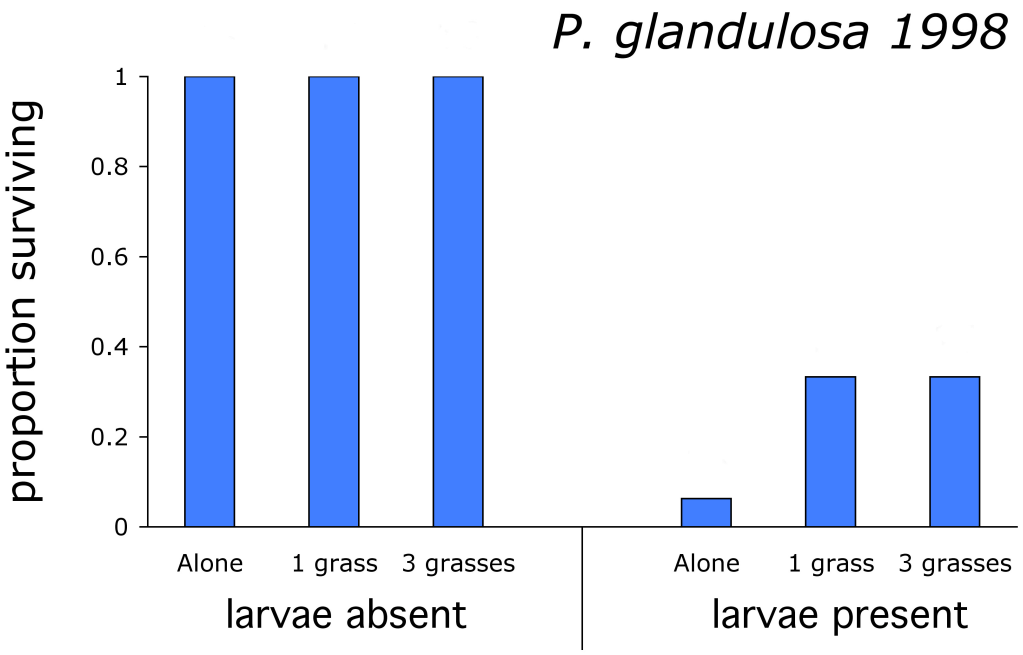



Figure 3.1. *Prosopis glandulosa* survival in 1998. Low and high grass density treatments were 1 and 3 *Schizachyrium scoparium* plants per pot, respectively. Larvae were absent or present at 4 per pot. There was no mortality of seedlings in pots with no *Phyllophaga spp.* larvae. Herbivory had a highly significant effect on seedling survival (chi-square test, $\chi^2$ = 57.8, df = 1, P < 0.0001). In each treatment with larvae absent, n=16 for each level of competition; in treatments with larvae present, n=16, 12, and 15 for seedlings grown in pots alone, with low grass density, and with high grass density, respectively.

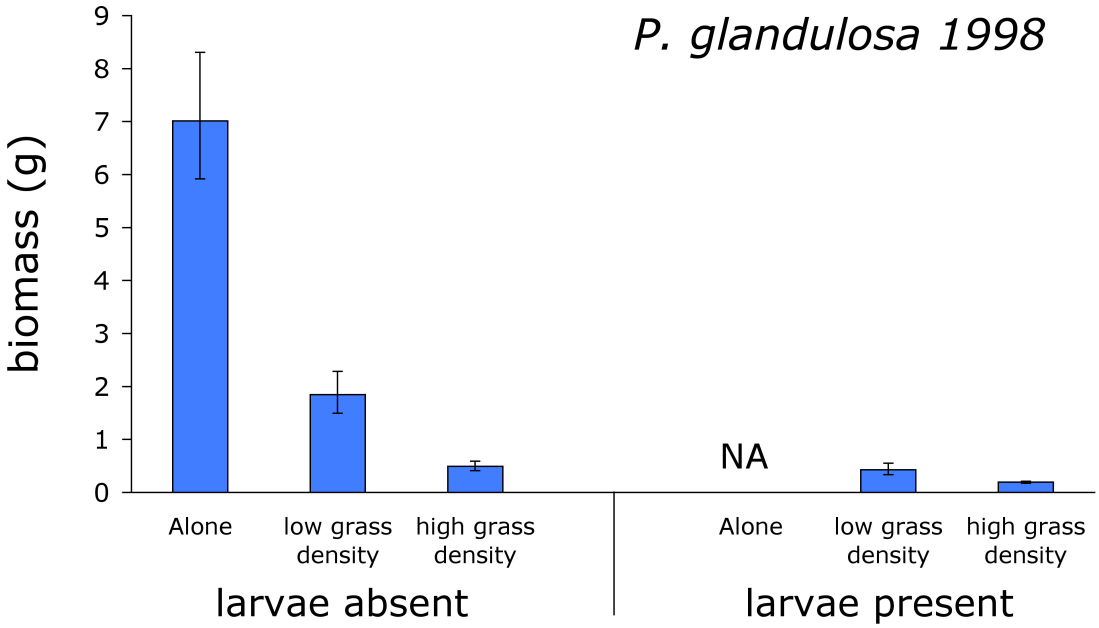



Figure 3.2. Total biomass (mean ± 1 SE) of *Prosopis glandulosa* seedlings in 1998. Low and high grass density treatments were 1 and 3 *Schizachyrium scoparium* plants per pot, respectively. Larvae were absent or present at four per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Only one of 16 seedlings grown alone with grubs survived and therefore were not included in the analysis. See Table 3.1 for statistical analysis for these data and see Figure 3.1 for treatment sample sizes.

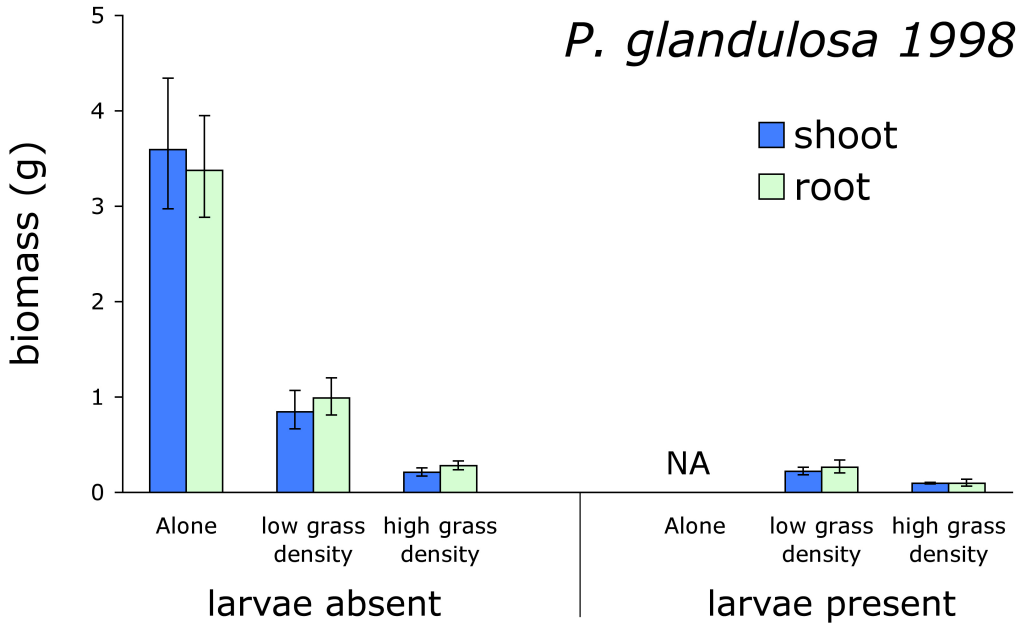



Figure 3.3. Shoot and root biomass (mean ± 1 SE) of *Prosopis glandulosa* seedlings in 1998. Low and high grass density treatments were 1 and 3 *Schizachyrium scoparium* plants per pot, respectively. Larvae were absent or present at four per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Only one of 16 seedlings grown alone with grubs survived and therefore were not included in the analysis. See Table 3.1 for statistical analysis for these data and see Figure 3.1 for treatment sample sizes.

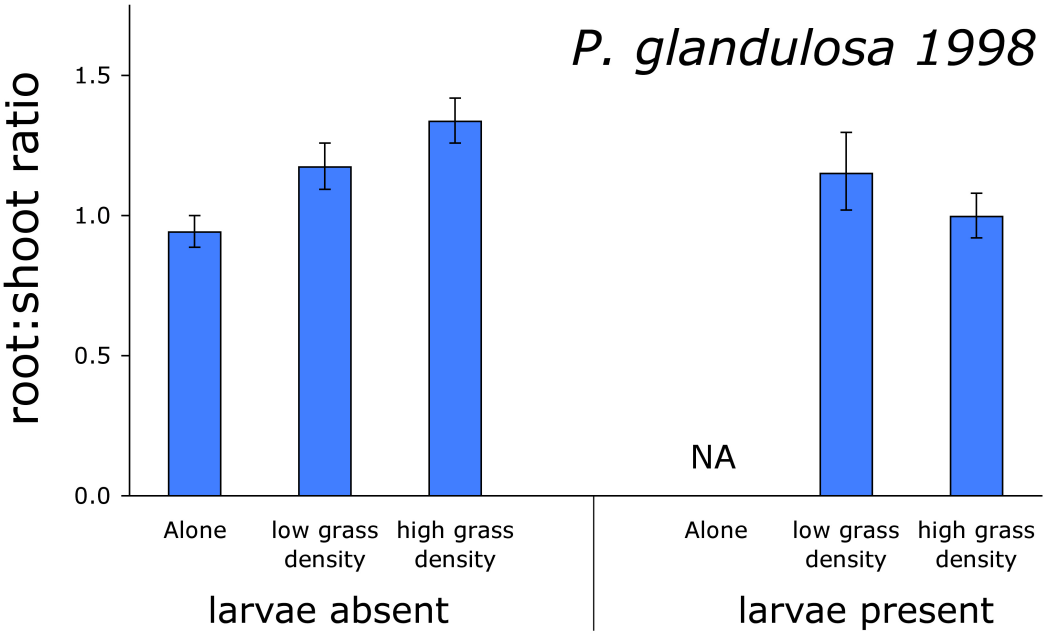



Figure 3.4. Root:shoot mass ratio (mean ± 1 SE) of *Prosopis glandulosa* seedlings in 1998. Low and high grass density treatments were 1 and 3 *Schizachyrium scoparium* plants per pot, respectively. Larvae were absent or present at four per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Only one of 16 seedlings grown alone with grubs survived and therefore were not included in the analysis. See Table 3.1 for statistical analysis for these data and see Figure 3.1 for treatment sample sizes.

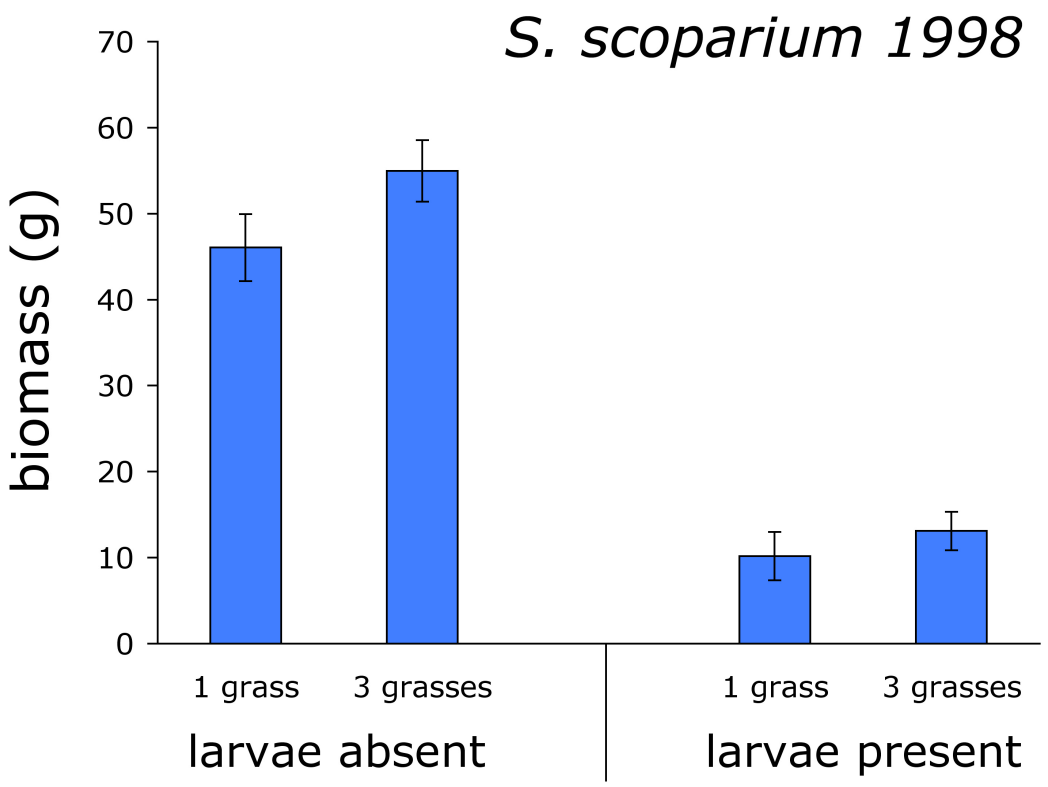



Figure 3.5. Mean (± 1 SE) of the summed biomass of all *Schizachyrium scoparium* in pots in 1998. These values were calculated by first summing the biomasses of the plants in a given pot, and then averaging all pots receiving the indicated treatment. Low and high grass density treatments were 1 and 3 *Schizachyrium scoparium* plants per pot, respectively. Larvae were absent or present at four per pot. Statistical analyses for these data are shown in Table 3.2.

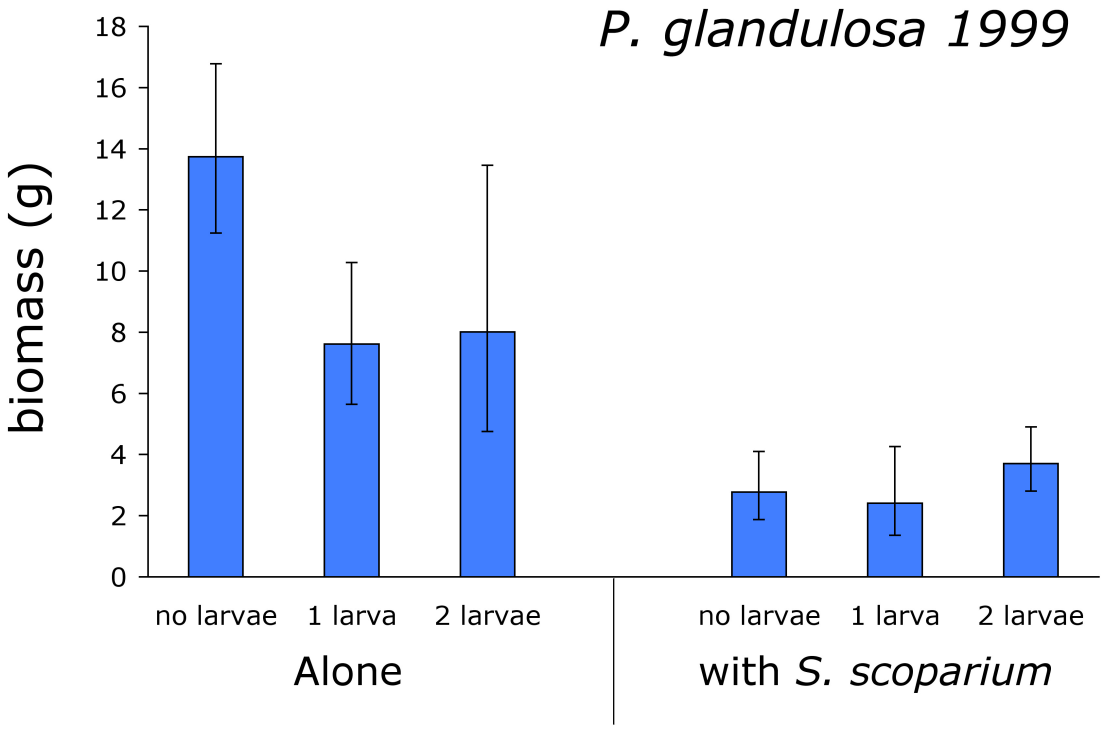



Figure 3.6. Total biomass (mean ± 1 SE) of *Prosopis glandulosa* seedlings in 1999. The levels of herbivory are 0, 1, and 2 larvae per pot. The levels of competition are 0 and 1 *Schizachyrium scoparium* plant per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Statistical analyses for these data are shown in Table 3.3.

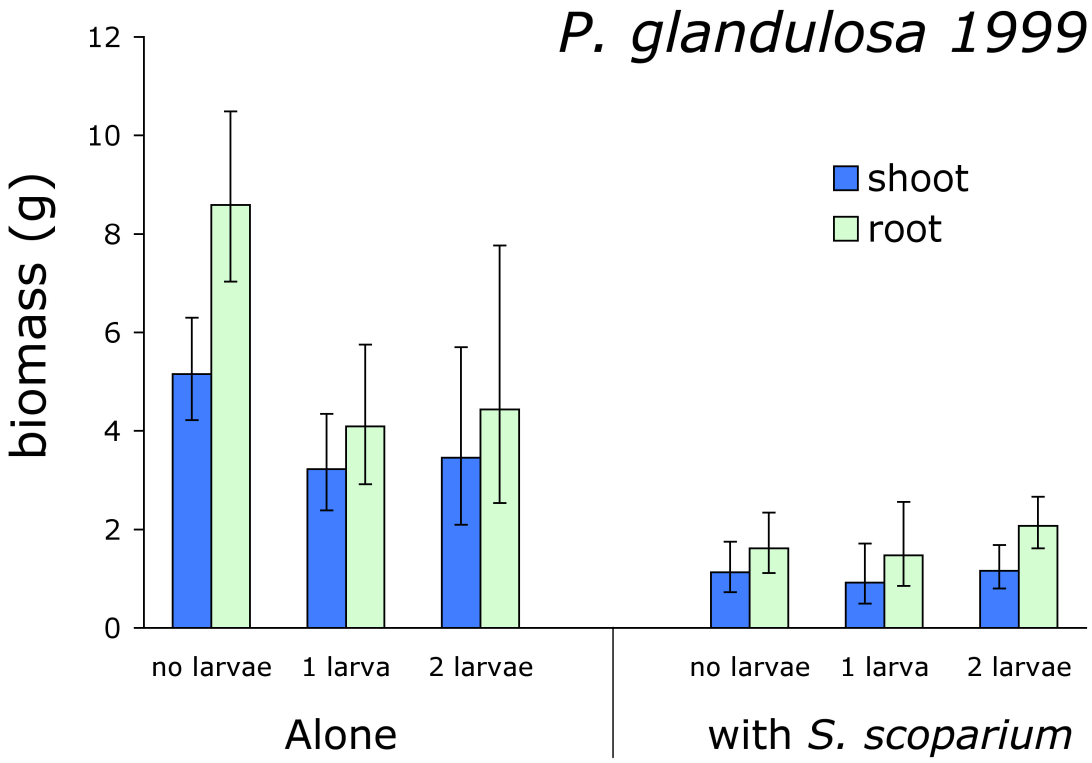



Figure 3.7. Shoot and root biomass (mean ± 1 SE) of *Prosopis glandulosa* seedlings in 1999. The levels of herbivory are 0, 1, and 2 larvae per pot. The levels of competition are 0 and 1 *Schizachyrium scoparium* plant per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Statistical analyses for these data are shown in Table 3.3.

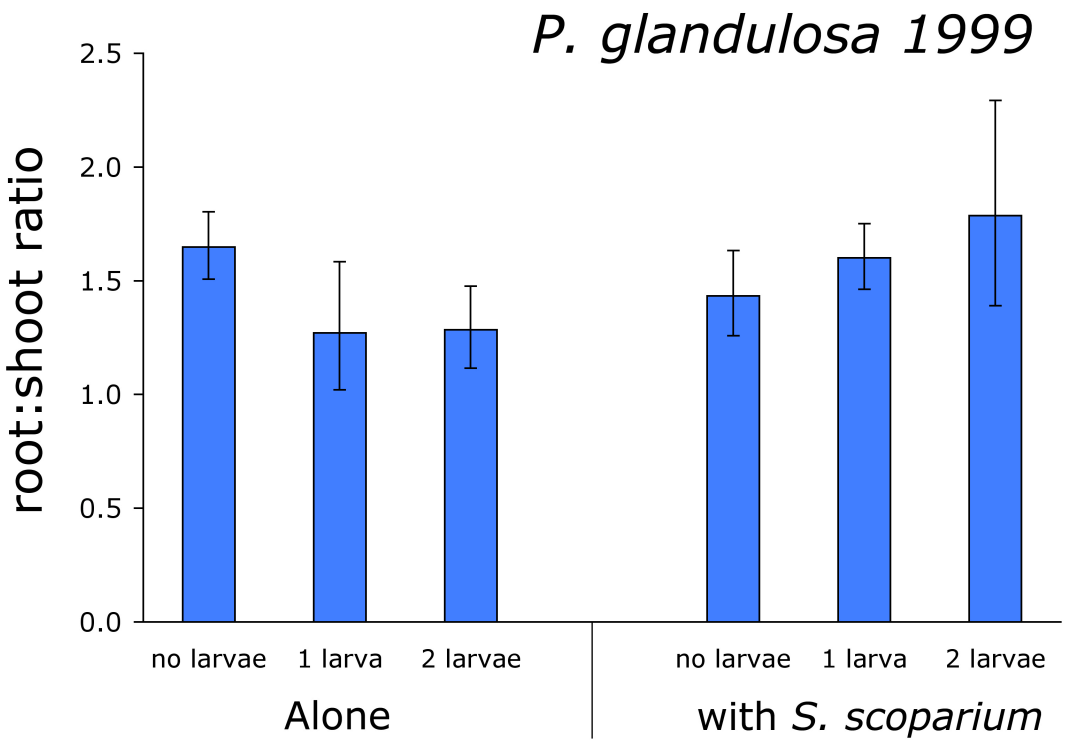



Figure 3.8. Root:shoot biomass ratio (mean ± 1 SE) of *Prosopis glandulosa* seedlings in 1999. The levels of herbivory are 0, 1, and 2 larvae per pot. The levels of competition are 0 and 1 *Schizachyrium scoparium* plant per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Statistical analyses for these data are shown in Table 3.3.

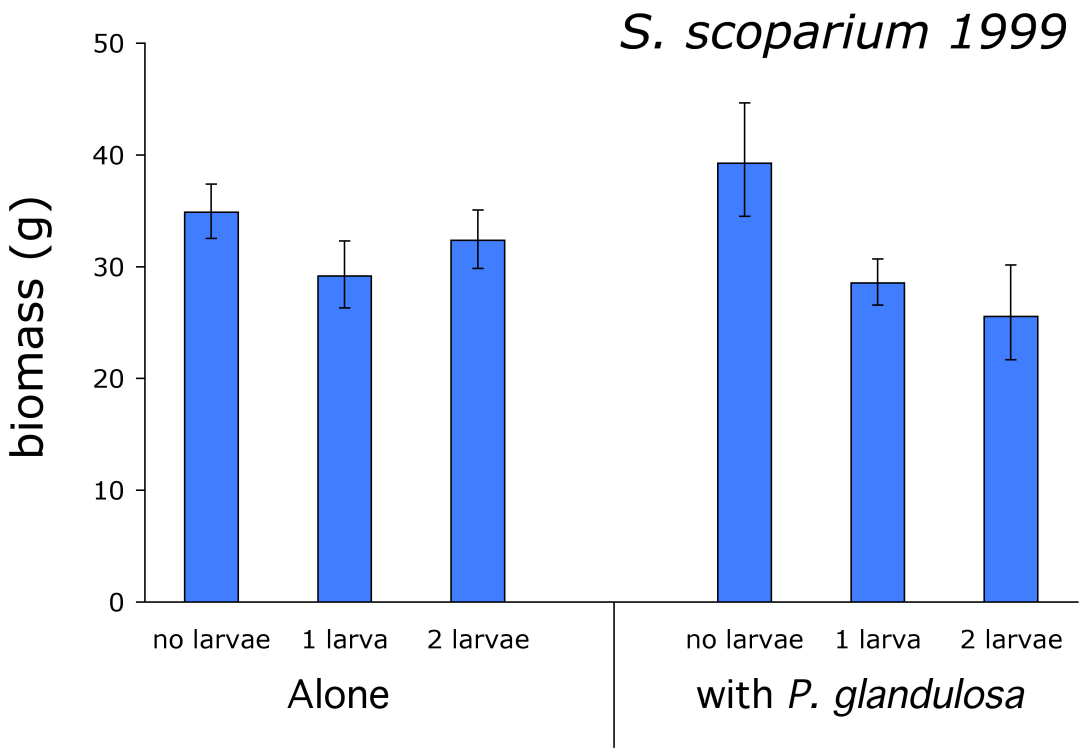



Figure 3.9. Total biomass (mean ± 1 SE) of individual *Schizachyrium scoparium* plants in 1999. The levels of herbivory are 0, 1, and 2 larvae per pot. The levels of competition are 0 and 1 *Prosopis glandulosa* plant per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Statistical analyses for these data are shown in Table 3.4.

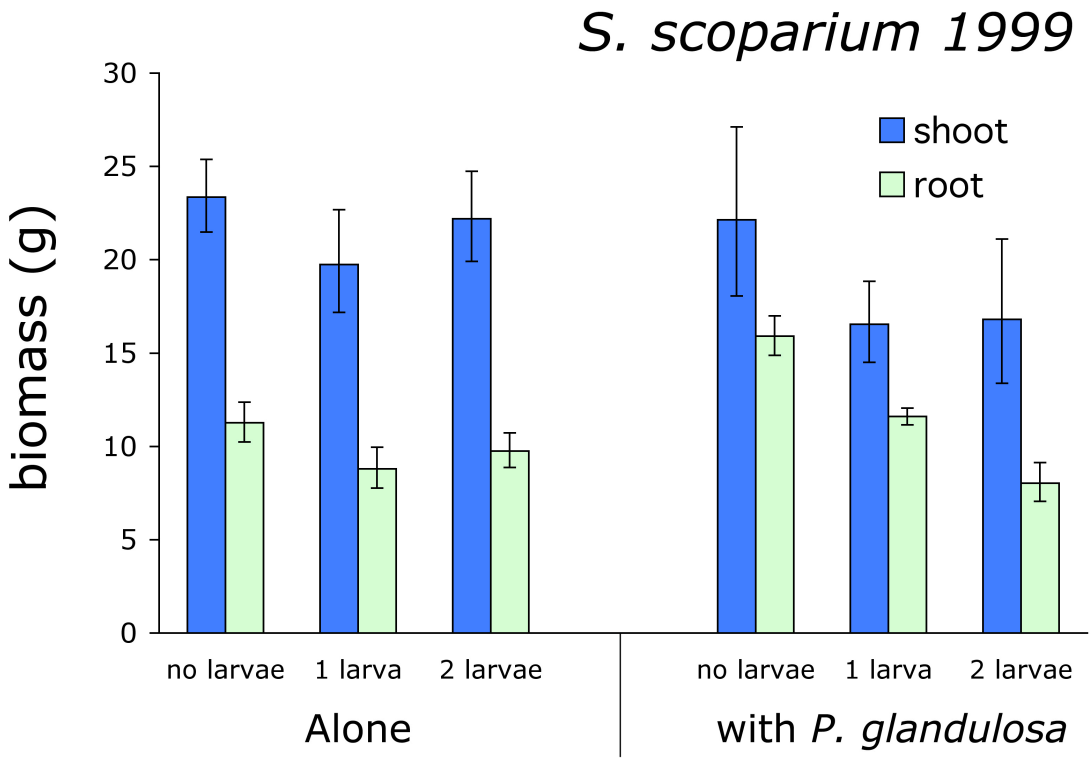



Figure 3.10. Shoot and root biomass (mean ± 1 SE) of *Schizachyrium scoparium* seedlings in 1999. The levels of herbivory are 0, 1, and 2 larvae per pot. The levels of competition are 0 and 1 *Prosopis glandulosa* plant per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Statistical analyses for these data are shown in Table 3.4.

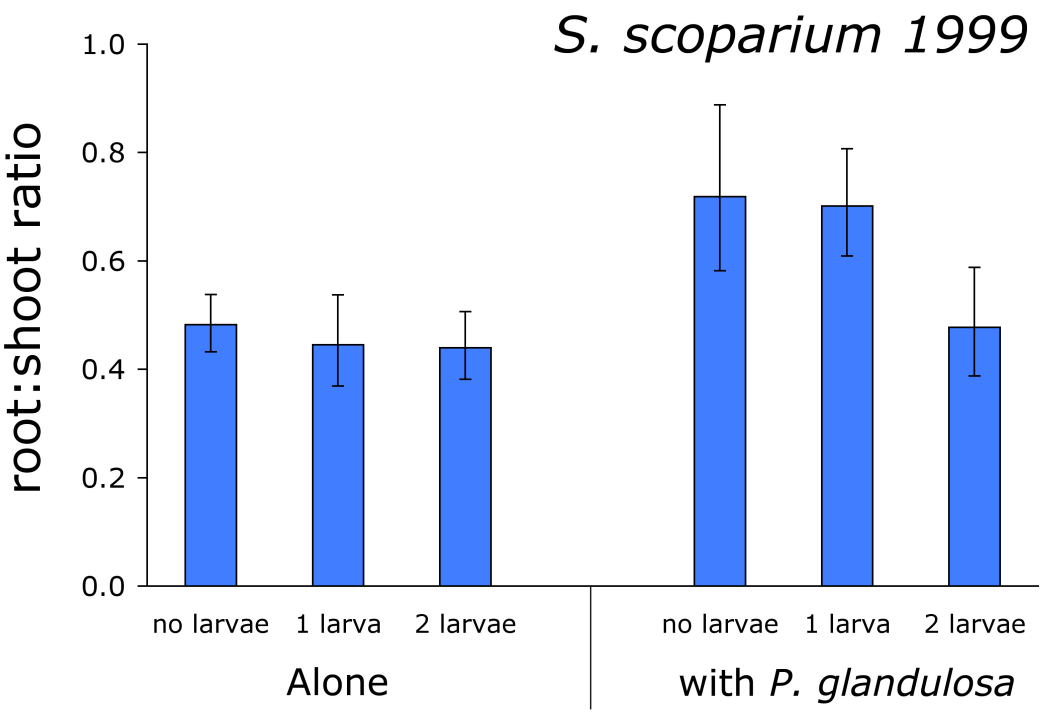



Figure 3.11. Root:shoot mass ratio (mean ± 1 SE) of *Schizachyrium scoparium* seedlings in 1999. The levels of herbivory are 0, 1, and 2 larvae per pot. The levels of competition are 0 and 1 *Prosopis glandulosa* plant per pot. Column heights are the back-transformed means of log-transformed values. Upper error bar=back-transformed ([mean + 1 S.E.] of log-transformed values); lower error bar= back-transformed ([mean - 1 S.E.] of log-transformed values). Therefore the upper and lower error bars are not symmetrical. Statistical analyses for these data are shown in Table 3.4.


Figure 3.12. Photo of *Schizachyrium scoparium* plants harvested at the completion of the 1998 study. The plant on the left was in a pot with no larvae; the plant on the right was in a pot with four *Phyllophaga spp.* larvae. Both grass plants shown were in low grass density pots (only one grass plant per pot).

Appendix A: Description of vegetation and soil at 12 survey sites located on the eastern Edwards Plateau in central Texas. All sites are located in Travis Co., except for Camp Creek Recreation Area which is located in Burnet Co. Plant species in bold type were present in surveyed plots; plants in non-bold type were prevalent in the surrounding areas, but not present in plots. Soil classifications and corresponding map sheets are from *Soil Survey of Travis County, Texas* (USDA Soil Conservation Service 1974) and from *Soil Survey of Blanco and Burnet Counties, Texas* (USDA Soil Conservation Service 1979).

| Site | Dominant Grasses | Common Woody Species | Soil Classification (Map and Soil Name) | Soil Description |
|---|---|---|---|---|
| **Barton Creek Preserve** | ***Schizachryium scoparium***<br>***Bothriochloa ischaemum***<br>*Bothriochloa saccharoides* | ***Carya illinoensis***<br>***Juniperus asheii***<br>*Prosopis glandulosa* | Map 51<br><br>Volente complex (VoD) | dark<br>loose<br>silty clay loam |
| **Brackenridge Field Lab** | ***S. scoparium***<br>***B. ischaemum***<br>***B. saccharoides***<br>***Cynodon dactylon*** | ***Eysenhardtia texana***<br>***J. asheii***<br>***Quercus fusiformis***<br>***P. glandulosa*** | Map 52<br><br>Hardeman soils (HdE) | reddish-brown<br>moderately loose<br>sand-silty loam |
| **Camp Creek Recreation Area** | ***S. scoparium***<br>***B. ischaemum***<br>*Aristida sp.* | ***Baccharis neglecta***<br>***Diospyros texana***<br>***J. asheii***<br>***Q. fusiformis***<br>***P. glandulosa*** | Map 30<br><br>Purves (PuC) | dark,<br>moderately heavy<br>stony-clay<br>frequent rocks |
| **Gloster Bend Recreation Area** | ***S. scoparium***<br>***B. ischaemum***<br>*B. saccharoides*<br>*Panicum virgatum* | ***B. neglecta***<br>***J. asheii***<br>***P. glandulosa***<br>*Q. fusiformis* | Map 11<br><br>Altoga (AgB) | dark<br>moderately loose<br>silty-clay |

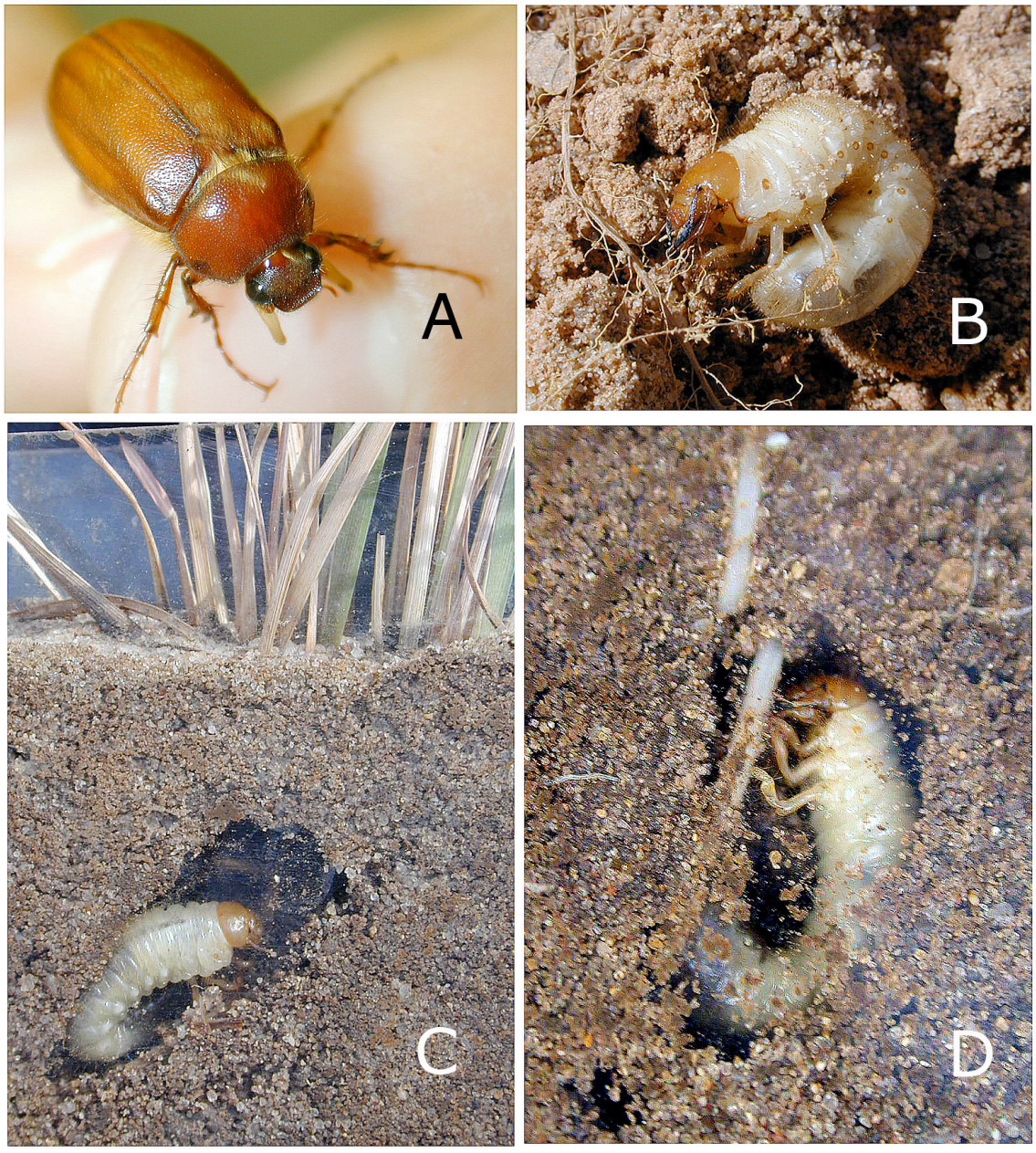
Appendix A (cont.): Description of vegetation and soil at 12 survey sites located on the eastern Edwards Plateau in central Texas. All sites are located in Travis Co., except for Camp Creek Recreation Area which is located in Burnet Co. Plant species in bold type were present in surveyed plots; plants in non-bold type were prevalent in the surrounding areas, but not present in plots. Soil classifications and corresponding map sheets are from *Soil Survey of Travis County, Texas* (USDA Soil Conservation Service 1974) and from *Soil Survey of Blanco and Burnet Counties, Texas* (USDA Soil Conservation Service 1979).

| Site | Dominant Grasses | Common Woody Species | Soil Classification (Map and Soil Name) | Soil Description |
|---|---|---|---|---|
| **Hamilton Pool Nature Preserve** | ***S. scoparium***<br>***B. ischaemum*** | ***P. glandulosa***<br>*J. ashei*<br>*Q. fusiformis* | Map 39<br><br>Volente complex (VoD) | dark,<br>moderately loose<br>silt-clay loam |
| **Lady Bird Johnson Wildflower Center** | ***S. scoparium***<br>***B. ischaemum***<br>*Curly mesquite* | ***Agarita tridentata***<br>***J. asheii***<br>***Q. fusiformis***<br>***Ulmus crassifolia*** | Map 67<br><br>Speck (SsC) | dark<br>moderately heavy<br>stony clay loam<br>frequent rocks |
| **Pace Bend Recreation Area** | ***S. scoparium***<br>***B. ischaemum***<br>***B. saccharoides***<br>***Aristida sp.*** | ***J. asheii***<br>***P. glandulosa***<br>*Q. fusiformis* | Map 20<br><br>Pedernales (PdC) | reddish<br>loose<br>fine sandy loam |
| **Porter Ranch** | ***S. scoparium***<br>***B. ischaemum***<br>***Aristida sp.*** | ***Bumelia lanuginosa***<br>***C. illinoensis***<br>***J. asheii***<br>***Q. fusiformis*** | Map 50 & 51<br><br>Volente complex (VoD) | dark<br>moderately loose<br>silt-clay loam<br>frequent rocks |

Appendix A (cont.): Description of vegetation and soil at 12 survey sites located on the eastern Edwards Plateau in central Texas. All sites are located in Travis Co., except for Camp Creek Recreation Area which is located in Burnet Co. Plant species in bold type were present in surveyed plots; plants in non-bold type were prevalent in the surrounding areas, but not present in plots. Soil classifications and corresponding map sheets are from *Soil Survey of Travis County, Texas* (USDA Soil Conservation Service 1974) and from *Soil Survey of Blanco and Burnet Counties, Texas* (USDA Soil Conservation Service 1979).

| Site | Dominant Grasses | Common Woody Species | Soil Classification (Map and Soil Name) | Soil Description |
|---|---|---|---|---|
| **Shield Ranch – Chalk Hill** | ***S. scoparium***<br>***B. ischaemum*** | ***D. texana***<br>***J. asheii***<br>***Q. fusiformis***<br>***Ziziphus jujuba*** | Map 50<br><br>Brackect soils (BlD) | light brown<br>moderately heavy<br>clay loam<br>frequent rocks |
| **Shield Ranch – Ungrazed** | ***S. scoparium***<br>*Muhlenbergia sp.* | ***A. tridentata***<br>***Celtis laevigata***<br>***D. texana***<br>***J. asheii***<br>***Q. fusiformis*** | Map 58<br><br>Brackect soils (BlD) /<br>Volente complex (VoD) | dark<br>moderately heavy<br>clay loam /<br>silty-clay loam |
| **Slaughter Tract** | ***S. scoparium***<br>***B. ischaemum*** | ***B. neglecta***<br>***B. lanuginosa***<br>***C. illinoensis***<br>***Illex vomitoria***<br>***P. glandulosa***<br>***Ulmus crassifolia***<br>*Q. fusiformis* | Map 67<br><br>Brackect soils (BlD) | dark<br>heavy<br>clay loam |
| **Slaughter Cemetery** | ***S. scoparium***<br>***B. ischaemum***<br>*B. saccharoides* | *Q. fusiformis*<br>*C. illinoensis*<br>*P. glandulosa* | Map 67<br><br>Volente complex (VoD) | dark<br>moderately loose<br>silt-clay loam |

Appendix B. Photos of adult and larval June beetles (*Phyllophaga crinita.*): adult male (A), third instar in typical C-shape (B), feeding on root (C), and feeding at the base of a little bluestem grass (*Schizachyrium scoparium*).



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